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AUTHOR(S):

NAKAYA, Hideo

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# FAUNAL CHANGE OF LATE MIOCENE AFRICA AND EURASIA: MAMMALIAN FAUNA FROM THE NAMURUNGULE FORMATION, SAMBURU HILLS, NORTHERN KENYA

Hideo NAKAYA

*Department of Earth Sciences, Kagawa University*

**ABSTRACT** The Namurungule Formation yields a large amount of mammals of a formerly unknown and diversified vertebrate assemblage of the late Miocene. The Namurungule Formation has been dated as approximately 7 to 10 Ma. This age agrees with the mammalian assemblage of the Namurungule Formation. Sedimentological evidence of this formation supports that the Namurungule Formation was deposited in lacustrine and/or fluvial environments. Numerous equid and bovid remains were found from the Namurungule Formation. These taxa indicate the open woodland to savanna environments. Assemblage of the Namurungule Fauna indicates a close similarity to those of North Africa, Southwest and Central Europe, and some similarity to Sub-Paratethys, Siwaliks and East Asia faunas. The Namurungule Fauna was the richest among late Miocene (Turolian) Sub-Saharan faunas. From an analysis of Neogene East African faunas, it became clear that mammalian faunal assemblage drastically has changed from woodland fauna to openland fauna during Astaracian to Turolian. The Namurungule Fauna is the forerunner of the modern Sub-Saharan (Ethiopian) faunas in savanna and woodland environments.

**Key Words:** Mammal; Neogene; Miocene; Sub-Saharan Africa; Kenya; Paleobiogeography; Paleocology; Faunal turnover.

## INTRODUCTION

### I. Scope of Study

#### 1. Late Miocene Gap of Sub-Saharan Mammalian Evolution

In evolutionary paleontology, the late Miocene is an important age for mammalian evolution. The modern mammalian fauna appeared from this age in Eurasia. In Sub-Saharan Africa, the assemblage of the late Miocene mammalian faunas was very poor, and these faunas were represented by only the Ngorora upper E, Ngeringerowa and Nakali faunas before the commencement of the Japan and Kenya joint expedition to the Samburu Hills, northern Kenya. Because of this incompleteness of the late Miocene East African faunas, it is very difficult to compare with Eurasian and Sub-Saharan faunas of this age.

#### 2. Hominoid Fossil

In the human evolution, it is very important to study the origin of hominid and paleoenvironments of hominoids evolution in the Sub-Saharan Africa, because there is a large possibility that the fossil evidence for branching of the Hominidae from the

Hominoidea will be discovered there. Furthermore, the paleoenvironmental change such as savannitisation seems to affect on the human evolution. The Namurungule Fauna is very important, from the viewpoint of the environmental change onto the hominoid evolution during the late Miocene. A hominoid fossil (Samburu large Hominoid) was discovered from the Namurungule Formation and it seems to be a possible common ancestor of the Hominidae and the African Apes (*Pan* and *Gorilla*) or the direct ancestor of the African Apes (Ishida et al, 1984).

### 3. Excavation of Samburu Hills, Northern Kenya (1980-1988)

Since the beginning of this century, many excavation teams visited and studied in Sub-Saharan Cenozoic sites, because Charles Darwin (1871) suggested that “*it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.*” in “*The Descent of Man and Selection in Relation to Sex*” (Chapter VI). Japan and Kenya excavation team (supported by the Japanese Ministry of Education, Science and Culture with its Grant-in-Aid for Overseas Scientific Survey) started to study Miocene sites in northern Kenya since 1980. The author joined this team as a vertebrate paleontologist since 1981. The excavation in the Samburu Hills was started from 1982 and we found new rich vertebrates sites including hominoid fossils from the Namurungule Formation. The author was a junior representative of the branch in Nairobi, Kenya of the Japan Society for Promotion of Science and a research student of the National Museums of Kenya from April, 1983 to March, 1984. And he investigated the middle to late Miocene Sites yielding vertebrate fossils of Kenya in 1983. And he has been also a member of the joint excavation team of Japan and Kenya as a vertebrate paleontologist from 1984 to 1986. This team excavated the Samburu Hills area in 1982 (Ishida, 1984), 1984, 1986, 1988 and Japanese team excavated the late Miocene Lake Albert area of Zaire in 1989 (Ishida & Yasui eds., 1992).

## II. Historical View of Mammalian Interchange between Africa and Eurasia

The Mesozoic mammalian remains of Africa were found from the late Triassic or early Jurassic of Lesotho (Clemens et al., 1979), the late Jurassic of Tanzania (Clemens et al., 1979), the middle Jurassic to late Cretaceous of Morocco (Sigogmeau-Russell et al. 1988) and the early Cretaceous of Cameroon (Jacobs et al., 1988). Eutherian mammals appeared in Africa from the late Paleocene. In the Paleocene and Oligocene, mammalian remains were found only from north and west Africa excluding Sub-Saharan area. After the Oligocene, a great number of mammalian fossil sites in Sub-Saharan Africa have been described and phylogeny of these taxa has been studied (reviewed in Maglio & Cooke eds., 1978). Many mammalian taxa immigrated into Sub-Saharan Africa. A great deal of studies have been published about the Neogene mammalian interchange between Africa and Eurasia (Thenius, 1972; Coryndon & Savage, 1973; Maglio, 1978; Thomas, 1979, 1981, 1984; Howell, 1980; Thomas et al., 1982; Adams et al., 1983; Savage & Russell, 1983; Bemor, 1983, 1986; Bemor & Hussain, 1985; Tassy, 1986).

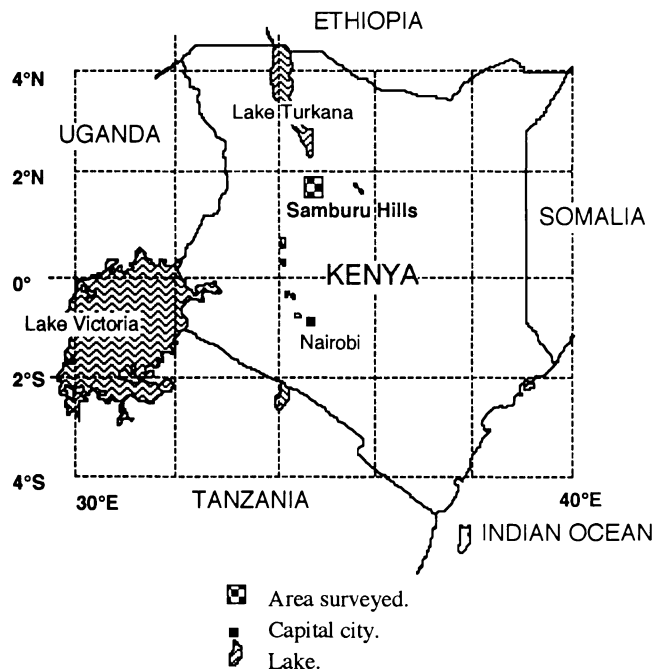
### III. Materials

The materials from the Samburu Hills are housed at the National Museums of Kenya (KNM) (Nairobi). The materials offered in this study were compared to African and Eurasian fossil mammals housed at the National Museums of Kenya (KNM) (Nairobi), British Museum (Natural History) (London), Laboratoire de Paléontologie, Muséum National d'Histoire naturelle (Paris), Laboratoire de Paléontologie des Vertébrés et de Paléontologie Humaine, Université de Paris VI (Paris), Department des Sciences de la Terre, Université Claude-Bernard, Lyon I (Villeurbanne) and Bayerischen Staatssammlung für Paläontologie und historische Geologie (München).

## GEOLOGICAL BACKGROUND

### I. Geology and Geochronology of the Namurungule Formation

The Samburu Hills form a belt about 30 km wide and about 80 km long trending in a north-southerly direction and beside the western wall of Suguta valley (Fig. 1).



**Fig. 1.** Locality map of the Samburu Hills.

The Neogene sediments and volcanics in the Samburu Hills consist of the Nachola, Aka Aiteputh, Namurungule, Nanyangaten, Kongia, Nagbarat and TIRR TIRR Formations (Fig. 2).

The Namurungule Formation yields a large amount of diversified vertebrates which appear to be of late Miocene in age thus belong to an assemblage heretofore unknown (Nakaya et al., 1984). Itaya & Sawada (in press) determined by K-Ar dating method the age of the Kongia and Nanyangaten Formations (5.7-7.3 Ma) clinounconformably overlying the Namurungule Formation and the Aka Aiteputh Formation (10-15 Ma) which underlies the Namurungule Formation. Consequently, the Namurungule Formation has been dated approximately as 8 to 10 Ma. This age agrees with the discovered mammalian assemblage of the Namurungule Formation (Nakaya et al., in press). Five paleomagnetic-zones were identified in the Samburu Hills. The Aka Aiteputh Formation is correlated to paleomagnetic-zone V in the period between 9.78 Ma and 10.3 Ma (Nakajima & Torii, in press).

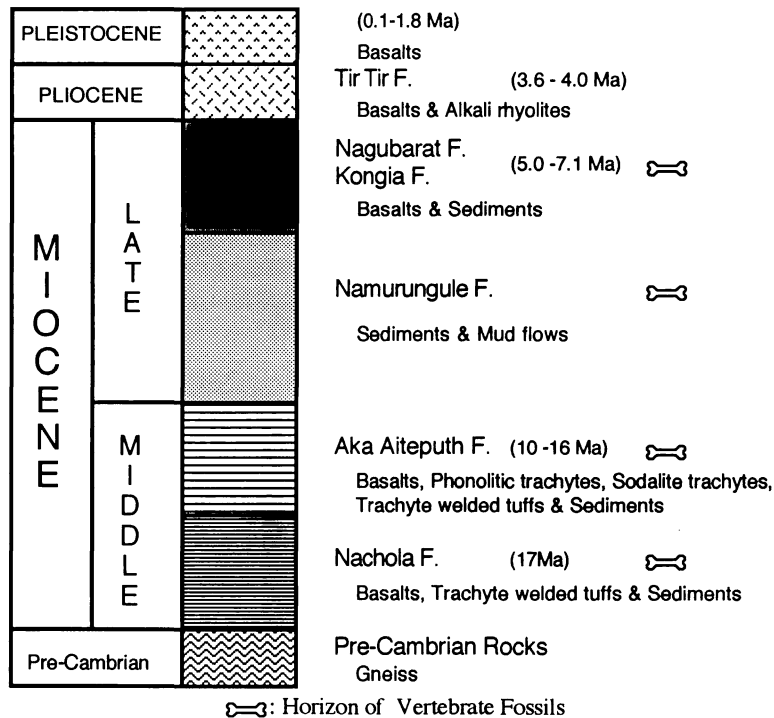


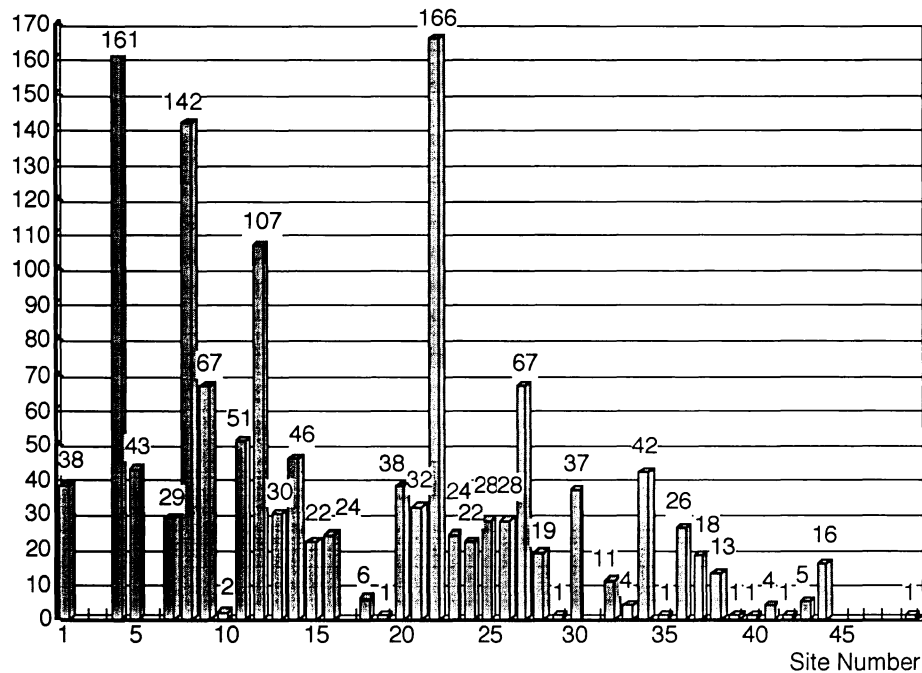
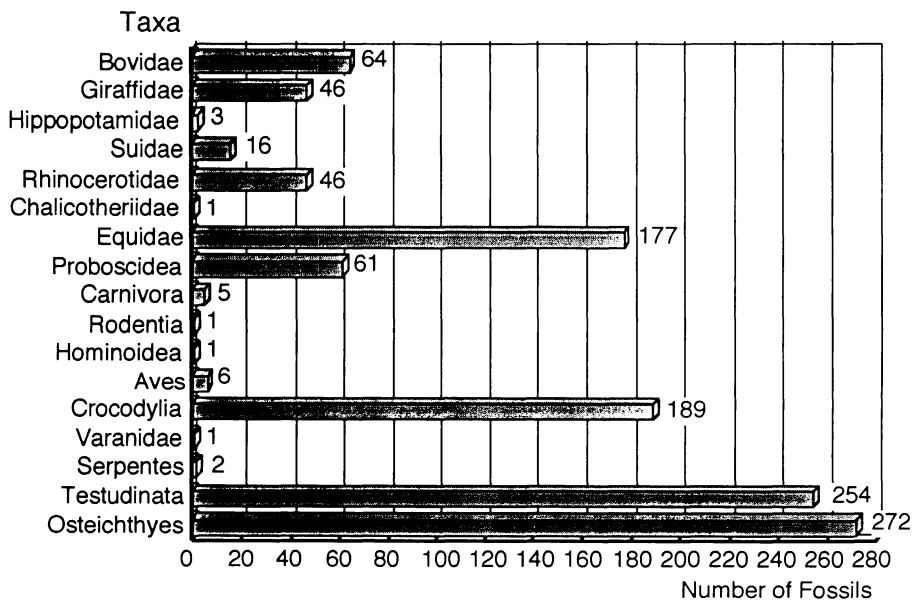
Fig. 2. Geology and geochronology of the Samburu Hills.

## II. Excavation of the Namurungule Formation

### 1. 1982 Excavation

Osaka University expedition team collected fossil remains on the surface of the Namurungule Formation of the Samburu Hills at random in 1982 field season. We excavated at the SH-22 of the locality of "Samburu Large Hominoid" in detail. Fossil numbers at each locality in the Namurungule Formation and number of taxa from the Namurungule Formation are shown in the following figures (Fig. 3, 4).

Number of Fossils

**Fig. 3.** Number of vertebrate fossils from each localities in the Samburu Hills.**Fig. 4.** Number of vertebrate taxa from the Namurungule Formation at 1982.

## 2. 1984 Excavation

In 1984 field season, Osaka University expedition team also collected fossil remains which were already surveyed in 1982 and newly discovered in 1984 randomly from the site surface of Samburu Hills and excavated locality SH-22 and some mammalian localities in detail.

## 3. 1986 Excavation

Osaka University expedition team also collected fossil remains which were already surveyed in 1984 randomly from the site surface of Samburu Hills in 1986 field season, and excavated locality SH-22 in detail. Fossil vertebrate localities show Figure 5.

## 4. 1988 Excavation

Osaka University expedition team also collected fossil remains which were already surveyed in 1986 randomly from the site surface of Samburu Hills in 1988 field season, and excavated locality SH-22 in detail by electric drilling machine.

## 5. Localities of Vertebrate Fossils and Stratigraphy of the Namurungule Formation

The Namurungule Formation consists of the Lower Member, Mud Flow, Upper Member in ascending order. The Lower Member consists of conglomerate, sandstone, thin mud flow deposits, pyroclastics, alternating beds of sandstone and mudstone predominantly in sandstone. The Mud Flow consists of reddish mud flow deposits 10-20 meter thick. The Upper Member consists of alternating beds of sandstone and mudstone predominantly in mudstone.

The Lower Member of Namurungule Formation yields the following vertebrate localities.

Locality SH-1, 7-9, 20-24, 26, 27, 30, 34, 40, 43, 44, 49-58, 61-64.

In the Upper Member of Namurungule Formation, we found the following vertebrate localities.

Locality SH-4, 5, 10-16, 18, 19, 25, 28, 29, 32, 33, 35-39, 41, 42, 60 (Fig. 5).

## 6. Taphonomy of Vertebrate Fossils in Situ

Almost all fossils were collected from the surface of the Namurungule Formation in the Samburu Hills. Some mammalian remains were excavated *in situ* of the Namurungule Formation in 1984. Almost all fossils were destroyed and weathered on the end position of skeleton because of the rolling before embedded in the deposits. For example, the skull of *Hipparion* from locality SH-53 was missing the incisive and occipital part. The mandible of *Deinotherium* from locality SH-54 was also missing the incisive, ventral border and ramus part. These remains were discovered in the overturned position in the sediments. The surface of some astragali of Giraffidae seems to be dissolved in acid solution. The surface shape of these astragali are different from that of rolled remains in the river. The edge of articular surface of these astragali is sharper than the original shape of articular part. The edge of articular surface of rolled remains in the river is rounded. These astragali remains may be stomach stones of crocodiles (Pickford, pers. comm.).

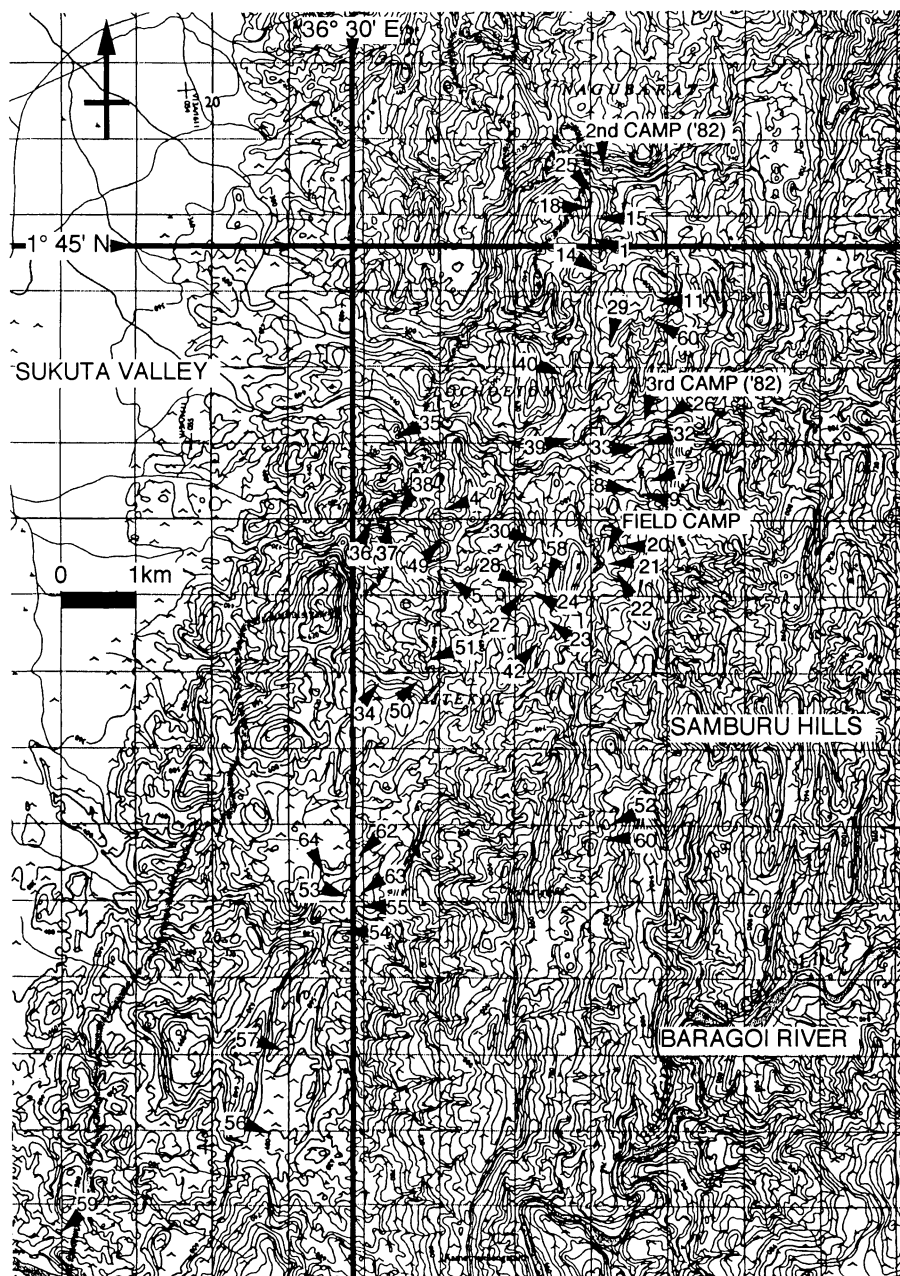


Fig. 5. Localities of vertebrate fossils in the Samburu Hills.

Topographic maps are based on sheets "Lobar" (65/1), "Kangaurak" (65/3), "Sukuta Valley" (64/2) and "Lomaro" (64/4) of series Y 731 (D.O.S. 423) 1:50,000 Topographic map published by D.O.S. for the Kenya Government (Survey of Kenya), 1982. Each grid is 1 km square.



## 7. Paleoenvironments of the Namurungule Formation

Sedimentological characteristics of the Namurungule Formation indicate lacustrine and fluvial environments (Makinouchi et al., 1984; Sawada et al., in press). Taphonomical evidence also assists such environments of the Namurungule Formation. The most abundant remains are fresh water fish. Crocodilian and chelonian fossils are also rich in the Namurungule Formation (Nakaya et al., 1984, in press; Pickford et al., 1984).

## THE NAMURUNGULE FAUNA

### I. Significance of the Namurungule Fauna

Three formations, the Aka Aiteputh, Namurungule, Kongia Formation, yield Neogene vertebrate fossils in the Samburu Hills. In this chapter, fossil assemblage and sedimentological facies of these formations are described.

#### 1. The Aka Aiteputh Fauna

This fauna is characterized by yielding abundant fossil primate remains (Pickford & Kuga, in press). The sedimentological facies indicates lacustrine environments, because the clastic sediments of the Aka Aiteputh Formation is mainly composed of fine sandstone and silt, and these fine sediments are partially silicified (Sawada et al., in press).

#### Mollusca

##### Gastropoda

##### Ampullariidae

##### *Lanistes carinatus*

##### Pomatiasidae

##### *Tropidophora (Ligatella) miocenica*

#### Bivalvia

##### Mutelidae

##### *Etheria elliptica*

#### Pisces

#### Reptilia

#### Crocodylia

##### Crocodylidae

##### gen. et sp. indet.

#### Testudines

##### Trionychidae

##### gen. et sp. indet.

##### Pelomedusidae

##### gen. et sp. indet.

#### Squamata

##### Serpentes

##### gen. et sp. indet.

#### Aves

gen. et sp. indet.  
Mammalia  
Primates  
  Cercopithecoidae  
    *Nyanzapithecus* sp.  
    *Victoriapithecus* sp.  
  Hominoidea  
    *Proconsul* sp.  
    *Kenyapithecus* cf. *africanus*  
Rodentia  
  *Paraphiomys* cf. *pigotti*  
Proboscidea  
  *Gomphotherium* sp.  
  *Prodeinotherium* sp.  
Perissodactyla  
  Rhinocerotidae gen. et sp. indet.  
Artiodactyla  
  Anthracotheriidae  
    *Hyoboops* sp.  
    *Hemimeryx* sp.  
  Sanitheriidae  
    *Diamantohyus africanus*  
Suidae  
  *Libycochoerus* sp. nov.  
Climacoceridae  
  *Climacoceras gentryi*  
Tragulidae  
  *Dorcatherium* cf. *pigotti*  
  *Dorcatherium chappusi*  
? Giraffidae ?  
  *Walangania africanus*  
Bovidae gen. et sp. indet

## 2. The Namurungule Fauna

The number of fossils of each taxon from the Namurungule Formation in 1982 excavation (Nakaya et al., 1984) is shown in Figure 4. for analyzing paleoenvironments of the fauna. Aqueous taxa (Pisces: Osteichthyes, Testudinata and Crocodylia) have numerous remains. This result supports the sedimentological and taphonomical evidence that the Namurungule Formation is lacustrine and/or fluvial in origin because of the predominant of the alternating bed and trough-type cross lamination of the coarse sediments (Sawada et al., in press). The appearance of numerous equids and bovids from the Namurungule Formation indicates the open country and/or woodland environments of the background (Nakaya et al., in press; Nakaya, 1987, 1989, 1993). Very large number of equid, giraffid and bovid remains shows that these taxa were social behavior animal. Very small number of chalicotheres remains shows that this taxa was solitary animal on the view of paleoecological point.

Mollusca  
Gastropoda  
    *Limicolaria* aff. *martensiana*  
    *Trochonanina* (*Bloyetia*) aff. *nyroensis*  
Pisces  
Reptilia  
Crocodylia  
    Crocodylidae  
        gen. et sp. indet.  
Testudines  
    Trionychidae  
        gen. et sp. indet.  
    Pelomedusidae  
        gen. et sp. indet.  
Squamata  
    Sauria  
        Varanidae  
            gen. et sp. indet.  
    Serpentes  
        gen. et sp. indet.  
Aves  
    gen. et sp. indet.  
Mammalia  
Primates  
    Hominoidea  
        Genus and species nov.  
Rodentia  
    Thryonomyidae  
        *Paraphiomys* sp.  
        *Paraulacodus* sp.  
    Hystricidae  
Carnivora  
    Hyaenidae spp.  
    Felidae  
        Machairodontinae  
            gen. et sp. indet.  
Proboscidea  
    Gomphotheriidae  
        *Tetralophodon* sp. nov.  
    Deinotheriidae  
        *Deinotherium* cf. *bozasi*  
Perissodactyla  
    Equidae  
        *Hipparion africanum*  
    Chalicotheriidae  
        gen. et sp. indet.  
    Rhinocerotidae

*Paradiceros mukirii*  
*Chilotheridium pattersoni*  
*Kenyatherium bishopi*  
 Iranotheriinae sp. nov.

## Artiodactyla

## Suidae

*Nyanzachoerus tulotos* (small form)  
*Nyanzachoerus kanamensis* (large form)

## Hippopotamidae

*Kenyapotamus coryndoni*

## Giraffidae

*Palaeotragus* sp. nov.  
*Samotherium* ? sp.

## Bovidae

*Pachytragus laticeps*  
*Miotragocerus* sp.  
*Ouzocerus* ? sp.  
*Gazella* spp.

## 3. The Kongia Fauna

Of this fauna, mammalian remains have not yet been investigated in detail. Studies are confined to geochronological aspects. This Formation indicates lacustrine and/or fluvial in origin because of the predominance of fine sandstone and silt, and the alternation of sandstone and silt (Sawada et al., in press). The following taxa indicate riverine habitats.

## Mollusca

## Gastropoda

*Burtoa nilotica*  
*Chlamydarion* aff. *haans*  
*Limicolaria* aff. *martensiana*  
*Trochonania* (*Bloyetia*) aff. *nyroensis*  
*Tropidophora* (*Ligatella*) aff. *anceps*  
*Cleopatra* aff. *africana*  
*Mellanoides tuberculata*

## Bivalvia

*Mutela* sp.

## Insecta

## Pisces

## Reptilia

## Squamata

## Sauria

## Varanidae

gen. et sp. indet.

## Artiodactyla

## Hippopotamidae

*Hippopotamus* sp.

## II. Phylogeny and Paleobiogeography of the Namurungule Fauna

In this chapter, habitat of each taxa from the Namurungule Fauna, first appearance of the world and Sub-Saharan Africa, and distribution in the late Miocene are described (Nakaya et al., 1984, in press; Nakaya, 1987, 1989, 1993).

### 1. Primates

Hominoidea gen. et sp. nov.

This taxon, so called "*Samburu Large Hominoid*", is represented by the left Maxilla with cheek teeth from the Lower Member of Namurungule Formation. Samburu Hominoid is very unique and it is probable that this taxon is a common ancestor of australopithecine of the Hominidae and African ape (*Pan* and *Gorilla*) of the Hominoidea (Ishida et al., 1984, Groves, 1989). First appearance of Hominoidea was *Aegyptopithecus* from late Oligocene, Fayum, Egypt (Szalay & Delson, 1979). First appearance of this superfamily from Sub-Saharan Africa was *Proconsul*, *Limnopithecus* from early Miocene Karungu (Simons et al., 1978). Distribution of this taxon in the late Miocene was only "*Samburu Hominoid*" from this fauna in Sub-Saharan Africa. It has been made clear that ramapithecine from late Miocene Eurasia and *Pongo* (Orang-Utan) shared same clade (Martin, 1986). Because of this point of view, it has to be stressed that new hominoid fossil from the Namurungule Formation fills in the missing link of human evolution.

### 2. Rodentia

Thryonomyidae

*Paraphiomys* sp.

One left mandible fragment with cheek teeth of *Paraphiomys* sp. from the Lower Member of Namurungule Formation occurs (Kawamura & Nakaya, 1984). First appearance of genus *Paraphiomys* was *P. simonsi* from Oligocene (25 Ma) of Fayum (Wood, 1968). First appearance of this taxon from Sub-Saharan Africa was *Paraphiomys pigotti* and *P. stromeri* from early Miocene (Lavocat, 1973). Only *P. occidentalis* is known from the late Miocene deposit of Morocco (Lavocat, 1961). Only one genus *Paraphiomys* is known.

*Paraulacodus* sp.

Only one isolated right upper incisor of *Paraulacodus* sp. is known from the Lower Member of Namurungule Formation (Kawamura & Nakaya, in press). First appearance of genus *Paraulacodus* is shown by *P. indicus* from the Chinji Formation of Pakistan (Flynn et al., 1983). First appearance of this taxon from Sub-Saharan Africa was represented by *Paraulacodus johanesi* from the late Miocene Chorora Formation of Ethiopia (Jacobs et al., 1980). Distribution of this genus in the late Miocene is represented by the Chorora and Namurungule Fauna only.

### 3. Carnivora

Hyaenidae spp.

Hyaenidae from the Upper and Lower Member of Namurungule Formation consists of three taxa, based on tooth size. These hyaenids are represented by the isolated lower cheek teeth or fragments of mandible, therefore, genus and species cannot be determined precisely (Nakaya et al., 1984, in press). First appearance of Hyaenidae is known from Orléanian (MN 4) in Europe (Savage & Russell, 1983). First appearance of this taxon from Sub-Saharan Africa is shown by the early Miocene of Fort Ternan (Savage, 1978). Distribution of this family in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Hendey, 1974; Savage, 1978; Savage & Russell, 1983; Schmidt-Kittler, 1976, 1987).

#### Felidae

##### Machairodontinae gen. et sp. indet.

Only one isolated lower canine of Machairodontinae is found from the Lower Member of Namurungule Formation (Nakaya et al., in press). First appearance of this taxon is known from Vallesian (MN 9) in Europe (Savage & Russell, 1983). First appearance of this subfamily from Sub-Saharan Africa is represented by this Namurungule occurrence. Distribution of this subfamily in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

#### 4. Proboscidea

##### Gomphotheriidae

##### *Tetralophodon* sp. nov.

One Proboscidean skull was excavated from the Lower Member of Namurungule Formation on 1984, and it is now under preparation in the National Museums of Kenya. This skull has typical cheek teeth of the genus *Tetralophodon*, because the intermediate molar with four lophs is characterized by tetralophodont cusp pattern. In comparing with the angle of the basicranium of *Tetralophodon* of Eurasia and of the Namurungule Fauna (Nakaya et al., in press), it is known that typical European *Tetralophodon* (Tobien, 1973a, 1973b, 1978) has a low angle of the basicranium, however, the Namurungule specimen has a high angle (Fig. 6). *Paratetralophodon* from the Siwaliks has also high angle of basicranium (Tassy, 1983). First appearance of genus *Tetralophodon* is known as *T. longirostris* from the Vallesian in Europe (Tobien, 1978). First appearance of this taxon from Sub-Saharan Africa is known as a Tetralophodont form gen. et sp. indet. from middle Miocene Ngorora Formation (member D) (Tassy, 1986). Distribution of this genus in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Tobien, 1978; Savage & Russell, 1983).

#### Deinotheriidae

##### *Deinotherium* cf. *bozasi*

A mandible and cheek teeth of *Deinotherium* are found from the Upper and Lower Member of the Namurungule Formation (Nakaya et al., 1984, in press). First appearance

of genus *Deinotherium* is known from the early Miocene of Eurasia. First appearance of Deinotheriidae from Sub-Saharan Africa is known as *Prodeinotherium hobleyi* from the early Miocene of Bukwa and Karungu and *Deinotherium* cf. *bozasi* from the late Miocene of Nakali and Namurungule Fauna. *D. bozasi* is distinguished from *P. hobleyi* in size and the morphology of skull and upper cheek teeth (Harris, 1973, 1975, 1976, 1978). *D. bozasi* is known from the late Miocene of East Africa and the Pliocene to Pleistocene of Sub-Saharan Africa (from Ethiopia to Mozambique) (Harris, 1977; Nakaya et al., in press). Distribution of this genus in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Osborn, 1936; Savage & Russell, 1983).

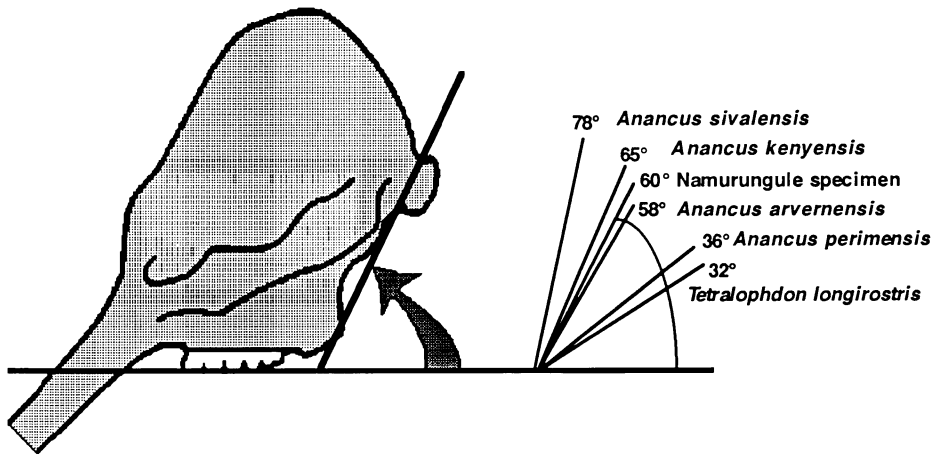


Fig. 6. Angle of tetralophodont basicranium (Modified after Tassy, 1983).  
left; measuring method of the angle of basicranium.  
right; angle of tetralophodont (*Tetralophodon* and *Anancus* group).

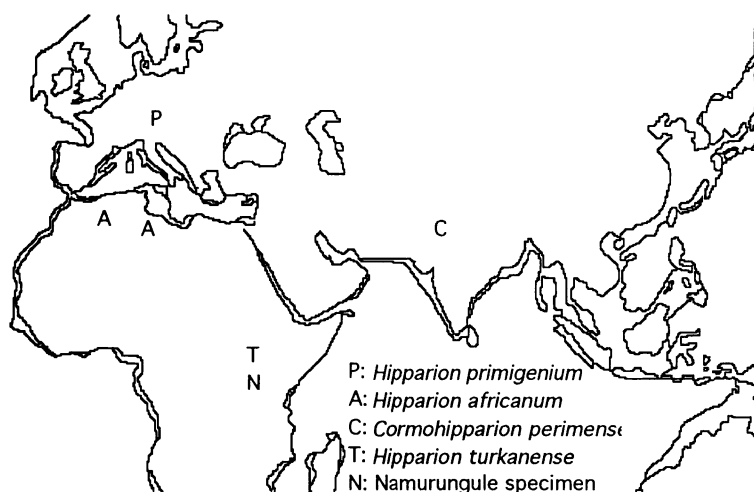
## 5. Perissodactyla

### Equidae

#### *Hipparion africanum*

The skull of hipparionine (Equidae) from the Upper and Lower Member of Namurungule Formation will be described and discussed by the author and Watabe, on its phylogenetic relationships with other African and Eurasian forms (Nakaya & Watabe, 1990). On the basis of the cranial morphology, especially preorbital fossa (POF) and dentition, this skull is similar to *Hipparion africanum* (Arambourg, 1959) from Bou Hanifia of North Africa of Vallesian age, and the proportions of slender limb bones from the Namurungule Formation is also comparable with those of the same *Hipparion*. Furthermore, this skull shows similarities to *Cormohipparion perimense* (Bernor & Hussain, 1985) from the Siwaliks on the basis of the morphology of antero-dorsally located POF. The age of *H. africanum* is older than the Namurungule Formation, and the age of the Dhok Pathan Formation of the Siwalik Hills yielding *C. perimense* is later than

that of the Namurungule Formation (Nakaya et al., in press). *Hipparion* suggests an open country habitat. First appearance of *H. africanum* is known from Vallesian of North Africa, *H. primigenium* was Vallesian Europe (Savage & Russell, 1983) and first appearance of *C. perimense* was in Siwaliks (Bernor & Hussain, 1985). First appearance of *H. africanum* from Sub-Saharan Africa was known from the Namurungule Formation. So called *Hipparion* found from Ngorora Formation first in Sub-Saharan Africa (Hooijer, 1975; 1976, Hooijer & Maglio, 1973, 1974; Bishop & Pickford, 1975; Pickford, 1978a). Figure 7 shows distribution of this genus in the late Miocene East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks, East and Central Asia and North America (Forstén, 1968, 1972, 1978, 1979, 1980a, 1980b, 1981, 1983, 1984; Eisenmann, 1977, 1979, 1982; Bernor & Hussain, 1985; MacFadden & Baker, 1979; MacFadden & Skinner, 1981; Singer & Boné, 1966; Woodburne & Bernor, 1980).



**Fig. 7.** Late Miocene fossil localities of large hipparionine from Africa and Eurasia.

#### Chalicotheriidae genus and species indeterminate

One basal phalange of the manus of Chalicotheriidae was collected from the Upper Member of Namurungule Formation (Nakaya et al., 1984). First appearance of this family is known from Sparnacian (Eocene) of Southwest Europe (Savage & Russell, 1983). First appearance of this taxon from Sub-Saharan Africa is *Chalicotherium rusingense* from early Miocene of East Africa. *Ancylotherium hennigi* was distributed from the late Miocene to early Pleistocene of East and South Africa (Butler, 1978). Distribution of this family in the late Miocene is known from East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

#### Rhinocerotidae

##### *Paradiceros mukirii*

Cheek teeth of brachyodont Rhinocerotidae *Paradiceros mukirii* were found from the



Lower Member of Namurungule Formation (Nakaya et al., in press). First appearance of *P. mukirii* is known from the middle Miocene of Fort Ternan (Hooijer, 1968). This genus includes only one species; only *P. mukirii* occurs at Fort Ternan in Kenya. Distribution of this taxon in the late Miocene is known from this fauna only (Hooijer, 1966, 1968, 1971, 1972, 1973).

*Chilotheridium pattersoni*

Cheek teeth of hypsodont Rhinocerotidae being indicated to *Chilotheridium pattersoni* were found from the Lower Member of Namurungule Formation (Nakaya et al., in press). First appearance of *C. pattersoni* is known from the early Miocene (Hooijer, 1971). This taxon ranges from the early to late Miocene of East Africa. Distribution of this taxon in the late Miocene is known from East Africa only (Hooijer, 1966, 1968, 1971, 1972, 1973, 1978).

*Kenyatherium bishopi*

Some cheek teeth of *Kenyatherium bishopi* were found from the Lower Member of Namurungule Formation (Nakaya et al., in press). *K. bishopi* is from late Miocene of Nakali of particular interest among Rhinocerotidae characterized by a constricted protocone (Aguirre & Guérin, 1974). This taxon belongs to the subfamily Iranotheriinae.

First appearance of this subfamily is known from the middle Miocene and it is represented by *Hispanotherium* from Iberian Peninsula (Crusafont-Pairo & de Villalta-Comella, 1947) and Turkey (Heissig, 1974), *Beliajevina* from Turkey (Heissig, 1974) and *Caementodon* from the Siwaliks (Heissig, 1972). Distribution of this subfamily in the late Miocene is represented by *Kenyatherium* from East Africa, *Iranotherium* from Iran (Mecquenem, 1908-1911) and *Sinootherium* from Northern China (Ringström, 1922, 1924, 1927) (Fig. 8).

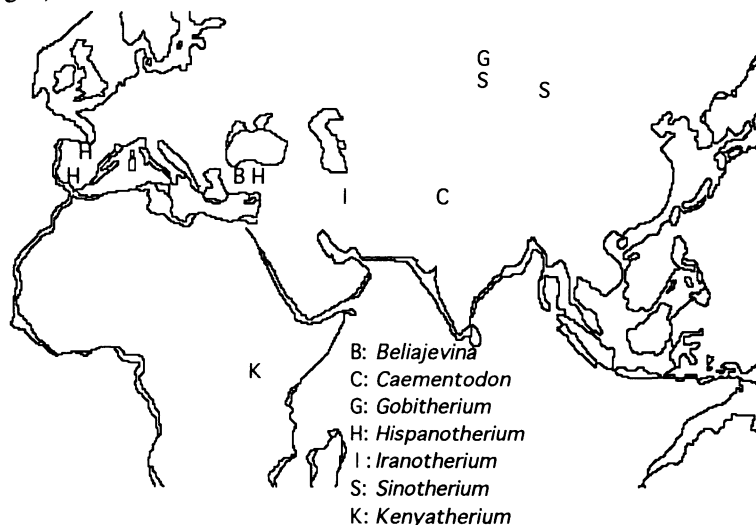


Fig. 8. Middle and late Miocene fossil localities of iranotheriine from Africa and Eurasia.

*Iranotheriinae* sp. nov.

Some specimens of the rhinocerotid from the Lower Member of the Namurungule Formation are not identified with any Sub-Saharan rhinocerotids (Hamilton, 1973b; Hooijer, 1966, 1968, 1971, 1972, 1973). *Kenyatherium bishopi* is similar to these materials on the basis of the morphology of cheek teeth. However, the cheek teeth of this taxon are larger than those of *K. bishopi* (Nakaya et al., in press), therefore, it appears from the above that these materials represent a new taxon.

## 6. Artiodactyla

## Suidae

*Nyanzachoerus tulotos*(small form)

*Nyanzachoerus kanamensis*(large form)

Two different species of *Nyanzachoerus* on the basis of the cheek teeth size, were found from the Upper and Lower Members of Namurungule Formation (Nakaya et al., in press). *Nyanzachoerus* suggests an open country habitat. First appearance of this genus is known from the late Miocene of Bou Hanifia (Algeria) (Arambourg, 1968). First appearance of this taxon from Sub-Saharan Africa is known from the Namurungule Formation. *Nyanzachoerus* was distributed in North and East Africa during the late Miocene (Arambourg, 1968; Bernor, 1986; Cooke & Ewer, 1972; Harris & White, 1979, White & Harris, 1977, Wilkinson, 1976).

## Hippopotamidae

*Kenyapotamus coryndoni*

Complete mandible and the cheek teeth of *Kenyapotamus* are found newly from the Upper and Lower Members of Namurungule Formation. *Kenyapotamus* includes only two species, *K. coryndoni* and *K. ternani*. Habitat of *Kenyapotamus* suggests on riverine habitat. First appearance of genus *Kenyapotamus* is known as *K. ternani* from the middle Miocene of Fort Ternan and Maboko of Kenya. *K. coryndoni* is known from late Miocene Ngeringerowa (Pickford, 1983) and the Namurungule Fauna only.

## Tragulidae

gen. et sp. indet.

A left talus of Tragulidae was found from the Upper Member of Namurungule Formation. Tragulidae suggests a forest habitat. First appearance of Tragulidae from Sub-Saharan Africa is known as *Dorcatherium chappuisi* from the early Miocene of Moruorot, Kenya (Whintworth, 1958). Distribution of this family in the late Miocene is known from Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

## Giraffidae

*Palaeotragus* sp. nov.

The giraffid's cheek teeth from the Upper and Lower Members of Namurungule Formation is similar to those of *Palaeotragus primaevus*, but the shape of hypocone of

upper molar of them is different from other species of Giraffidae in Africa (Nakaya et al., 1984, in press). *Palaeotragus* suggests a wooded open country habitat. First appearance of this genus is known as *P. primaevus* from the early Miocene of Moruorot, Kenya (Singer & Boné, 1960; Gentry, 1978a; Hamilton, 1973a, 1978). Distribution of this genus in the late Miocene is known as *P. germaini* from Lothagam, Kenya (Churcher, 1979) in East Africa.

*Samotherium*? sp.

Some limb bones of giraffid were obtained from the Upper and Lower Members of Namurungule Formation. They are larger than specimens of *Palaeotragus* (Nakaya et al., in press). These materials are identified as *Samotherium*? sp. *Samotherium* suggests a wooded open country habitat. First appearance of *Samotherium* is known from the middle Miocene of Pasalar, Turkey (Bernor & Pavlakis, 1987). First appearance of this taxon in Sub-Saharan Africa is known as *Samotherium africanum* from the middle Miocene of Fort Ternan (Churcher, 1978). Distribution of this genus in the late Miocene is known to extend to East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia (Savage & Russell, 1983).

Bovidae

*Pachytragus laticeps*

Horn cores, compressed oval in section and curved uniformly, but gently backwards toward the tip, are discovered from the Lower Member of Namurungule Formation. They are identified as *Pachytragus laticeps* (Nakaya et al., 1984, in press and this work). This species was taxonomically revised to *Protoryx laticeps* by Solounias (1981). First appearance of *Pachytragus* and/or *Protoryx* is known from the late Miocene North Africa and Sub-Paratethys (Solounias, 1981; Savage & Russell, 1983). *Pachytragus* suggests an open country habitat. First appearance of this taxon from Sub-Saharan Africa confines to the Namurungule Formation. Distribution of this taxon in the late Miocene is *P. solignaci* from Beglia (Robinson, 1972) and the Namurungule Fauna in Africa. This genus group is widely known from Afro-Eurasia (East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia) during the late Miocene (Savage & Russell, 1983).

*Miotragocerus* sp.

A horn core, curved and spiral with an anterior keel, from the Lower Member of Namurungule Formation is identified as *Miotragocerus* (Nakaya et al., 1984). First appearance of this genus was Astaracian (Savage & Russell, 1983). *Miotragocerus* suggests an open country habitat. First appearance of this taxon from Sub-Saharan Africa is known from the Namurungule Fauna. This genus is known from Afro-Eurasia widely (East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia) during the late Miocene (Savage & Russell, 1983).

**Table 1.** Faunal resemblance of the Namurungule Fauna and Eurasian faunas.

Mammalia	
Primates	
Hominoidea	
Genus and species nov.	A
Rodentia	
Thryonomyidae	
<i>Paraphiomys</i> sp.	A
<i>Paraulacodus</i> sp.	S
Carnivora	
Hyaenidae spp.	E
Felidae	
Machairodontinae	
gen. et sp. indet.	E
Proboscidea	
Gomphotheriidae	
<i>Tetralophodon</i> sp. nov.	E
Deinotheriidae	
<i>Deinotherium</i> cf. <i>bozasi</i>	E
Perissodactyla	
Equidae	
<i>Hipparion africanum</i>	N
Chalicotheriidae	
gen. et sp. indet.	E
Rhinocerotidae	
<i>Paradiceros mukirii</i>	A
<i>Chilotheridium pattersoni</i>	A
<i>Kenyatherium bishopi</i>	A
Iranotheriinae sp. nov.	A
Artiodactyla	
Suidae	
<i>Nyanzachoerus tulotos</i> (small form)	N
<i>Nyanzachoerus kanamensis</i> (large form)	N
Hippopotamidae	
<i>Kenyapotamus coryndoni</i>	A
Giraffidae	
<i>Palaeotragus</i> sp. nov.	E
<i>Samotherium</i> ? sp.	E
Bovidae	
<i>Pachytragus laticeps</i>	P
<i>Miotragocerus</i> sp.	E
<i>Ouzocerus</i> ? sp.	N,P
<i>Gazella</i> spp.	E

Notes: A: unique Sub-Saharan taxa; N: common with North Africa taxa; P: common with Sub-Paratethys taxa; S: common with Siwalik taxa; E: common with Eurasia taxa.

*Ouzocerus*? sp.

Skull and horn cores that are nearly circular in section with a sharp posterior keel, from the Upper and Lower Members of Namurungule Formation are identified as *Palaeoreas* sp. (Nakaya et al., 1984). However *Ouzocerus* described newly is more similar to this specimen (this work). This genus includes only one species, *O. gracilis*, and is known from Vallesian of northern Greece for the first time (Bouvrain & Bonis, 1986) and the late Miocene Beglia Formation of Tunisia (Thomas, pers. comm.). First appearance of this taxon from Sub-Saharan Africa is known from the Namurungule Formation. Distribution of this taxon is known from East and North Africa and Sub-Paratethys during the late Miocene.

*Gazella* sp.

Some horn cores of *Gazella* were discovered from the Upper and Lower Member of Namurungule Formation (Nakaya et al., 1984, in press). This genus includes many species. *Gazella* suggests an open country habitat. First appearance of this genus is known from the early Miocene of Gebel Zelten, North Africa (Hamilton, 1973a). First appearance of this taxon from Sub-Saharan Africa is known as *Gazella* sp. from the middle Miocene of Fort Ternan (Gentry, 1978b). This genus is known from Afro-Eurasia widely (East and North Africa, Southwest and Central Europe, Sub-Paratethys, Siwaliks and East Asia) during the late Miocene (Gentry, 1966, 1967, 1970, 1971, 1978a, b, 1980; Gentry & Gentry, 1978; Savage & Russell, 1983).

Resemblance of the Namurungule Fauna and other Eurasian faunas is shown in the Table 1.

### III. Correlation and Resemblance of Neogene Mammalian Faunas of Sub-Saharan Africa and Eurasia

#### 1. Late Miocene faunas of North Africa and Eurasia

In this chapter, the author describes typical late Miocene (Astaracian, Vallesian and Turolian) faunas of North Africa and Eurasia for the sake of making comparison with mammalian faunas of Sub-Saharan Africa.

##### (1) Eurasia (Western)

West Eurasian Neogene mammals have been studied since the eighteenth century. Ages of the Eurasian Neogene mammal and fossil assemblage zones in Southwestern Europe, Greece and Iran were revised by Savage & Russell (1983). The following five mammalian ages and 13 mammalian zones during the Miocene and two ages and four zones during the Pliocene were established respectively by them.

##### Miocene

##### Agenian (20-25 Ma)

MN 1

MN 2a

MN 2b

## Orleanian (15-20 Ma)

MN 3a

MN 3b

MN 4a

MN 4b

MN 5

## Astaracian (12-15 Ma)

MN 6

MN 7

MN 8

## Vallesian (10-12 Ma)

MN 9

MN 10

## Turolian (5-10 Ma)

MN 11

MN 12

MN 13

## Pliocene

## Ruscinian (-5 Ma)

MN 14

MN 15

## Villafranchian (2- Ma)

MN 16a

MN 16b

MN 17

## (2) Siwaliks

Falconer & Cautley (1846-1849) started the study of geology and paleontology of the Siwalik Hills. Pilgrim (1913) divided mammalian faunas and strata of the Siwaliks into seven stages and correlated them to the standard Neogene stages in Europe. Colbert (1935) revised Pilgrim's correlation and compared it to equivalents in Europe and America. In 1960's, *Ramapithecus* from the Siwaliks was reevaluated as a human ancestor (Simons, 1961). During 1950-1970s, many teams (Dehm et al., 1958; Pilbeam et al., 1977) excavated again at the Siwalik Hills. Research on faunal assemblage (Pilbeam et al., 1977; Moonen et al., 1978) and phylogenetic studies of each taxa have been published (Dehm et al., 1958, 1963; Hussain, 1971; Heissig, 1972; Jacobs, 1978; Tassy, 1983; Pickford, 1988), and geochronological data of strata of this area were obtained. The results of stratigraphic study of Siwaliks are shown in the following table (Pilbeam et al., 1977; Opdyke et al., 1979).

## Miocene

Kamlial (before 13 Ma; Pilbeam et al., 1977)

Chinji (11-13 Ma; Pilbeam et al., 1977)

Nagri (9-10 Ma; Pilbeam et al., 1977)

Dhok Pathan (6.5-9 Ma; Pilbeam et al., 1977)

## Pliocene

Tatrot (before 2.47 Ma; Opdyke et al., 1979)

Pinjor (after 2.47 Ma; Opdyke et al. 1979)

### (3) China

Many researchers studied Chinese Neogene terrestrial mammals and furthermore, Quaternary mammals with *Sinanthropus pekinensis* (*Homo erectus*) until 1940's (Andersson, 1923; Bohlin, 1937; Koken 1885; Ringström, 1922, 1924, 1927; Schlosser, 1924; Teilhard de Chardin, 1926; Teilhard de Chardin & Young; 1930, 1931; Zdansky, 1930). Researchers of the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing) began again to study fossil vertebrates from China since 1948. Cenozoic terrestrial stratigraphy in China was revised by Yen et al. eds., (1984). Established Neogene terrestrial zones of mammals in China are as follows.

#### Early Miocene

Xiejean (19-24 Ma)

#### Middle Miocene

Shanwangian (15-19 Ma)

Tungurian (12-15 Ma)

#### Late Miocene

Bahean (9-12 Ma)

Baodean (5-9 Ma)

#### Pliocene

Gaozhuangian

Youhean

Nihewanian

The following typical faunas from Astaracian to Turolian Sub-Saharan Africa and Eurasia treated in the next chapter have been correlated as shown in Table 2.

**Table 2.** Astaracian to Turolian typical mammalian localities from Sub-Saharan Africa and Eurasia.

MIOCENE Ma			East Africa	North Africa	West & Central Europe	Sub-Paratethys	Siwaliks	North China
L A T E	Turolian	5	Lukeino Mpesida	Sahabi				Yushe I
			Namurungule				Dhok Pathan	Baode
	Vallesian	10	Ngeringerowa Nakali Ngorora E		Mt. Lebéron	Samos Maragheh Pikermi	Nagri	
M I D D L E	Astaracian	12	Ngorora Aka Aiteputh	Bou Hanifia			Chinji	

## 2. North Africa

Many localities of mammalian fauna are known from the late Miocene of North Africa. The following mammalian faunas are represented as Vallesian faunas (Beglia and Bou Hanifia) and Turolian fauna (Sahabi).

### (1) Beglia (Tunisia)

This fauna is correlated to Vallesian fauna (MN 9) of North Africa. Some bovid taxa of this fauna are similar with those of the Namurungule Fauna. Faunal list of the Beglia Formation is as follows (Robinson, 1972; Robinson & Black, 1969; Thomas, pers. comm.).

#### Mammalia

##### Rodentia

*Africanomys* sp.

*Testouromys* sp.

*Mellalomys atlati*

##### Creodonta

Hyaenodontidae gen. et sp. indet.

##### Carnivora

Mustelidae gen. et sp. indet.

##### Hyaenidae

*Ictitherium* sp.

##### Felidae

*Machairodus* sp.

##### Canidae

*Afrocyon* sp.

##### Sirenia

gen. et sp. indet

##### Artiodactyla

##### Bovidae

*Pachytragus solignaci*

*Ouzocerus* sp.

### (2) Bou Hanifia, Oued-el-Hammam (Algeria)

This fauna is a typical Vallesian fauna (MN 9) in North Africa. Faunal list of the Bou Hanifia Fauna is as follows (Arambourg, 1959).

#### Aves

*Struthio* sp.

#### Mammalia

##### Primates

##### Cercopithecidae

*Macaca flandrini*

##### Rodentia

##### Hystricidae

*Hystrix* sp.

##### Carnivora

##### Hyaenidae



*Hyaena algeriensis*  
 Tubulidentata  
*Orycteropus mauritanicus*  
 Proboscidea  
 gen. et sp. indet.  
 Perissodactyla  
 Equidae  
*Hipparion africanum*  
 Rhinocerotidae  
*Dicerorhinus primaevus*  
 Artiodactyla  
 Giraffidae  
*Palaeotragus germaini*  
*Samotherium* sp.  
 Bovidae  
*Damalavus boroccoi*  
*Gazella praegaudryi*  
*Tragocerus* sp.  
*Cephalophus* sp.

### (3) Sahabi (Libya)

This fauna is a typical Turolian fauna in North Africa. Richness of equid and bovid taxa indicates open-country fauna. Faunal list of the Sahabi Fauna is as follows (Boaz et al. eds., 1987).

Insectivora  
 Soricidae  
 Crocidurinae gen. et sp. indet.  
 Primates  
 Hominoidea gen. et sp. indet.  
 Cercopithecidae  
 cf. *Libypithecus* sp.  
*Macaca* sp.  
 Rodentia  
 Sciuridae  
 cf. *Atlantoxerus getulus*  
 Ctenodactylidae  
*Sayimys* sp.  
 Cricetidae  
 aff. *Myocricetodon cherifensis*  
*Protatera yardangi*  
 Muridae  
*Progonomys* sp.  
 Cetacea  
 Delphinidae  
 cf. *Lagenorhynchus* sp.  
 Platanistidae gen. et sp. indet.

## Carnivora

## Ursidae

*Indarctos atticus**Agriotherium* cf. *africanum*

## Viverridae

*Viverra* sp.

## Hyaenidae

*Percrocuta eximia**Percrocuta senyueki**Hyaenictitherium* sp.*Euryboas* sp.

## Felidae

*Machairodus* sp.

sp. A

sp. B

sp. C

## Phocidae

aff. *Monachinae* gen. et sp. indet.

## Proboscidea

## Gomphotheriidae

*Amebelodon cyrenaicus*

## Elephantidae

*Stegotetrabelodon lybicus*

## Sirenia

## Dugongidae

*Metaxytherium serresii*

## Perissodactyla

## Equidae

"Hipparion" cf. *africanum*"Hipparion" cf. *sitifense*

## Rhinocerotidae

*Diceros neumayri*

## Artiodactyla

## Suidae

*Nyanzachoerus* cf. *devauxi**Nyanzachoerus syrticus**Nyanzachoerus kanamensis*

## Anthracotheriidae

*Merycopotamus petrocchii*

## Hippopotamidae

*Hexaprotodon sahabiensis*

## Giraffidae

*Samotherium* sp.

## Bovidae

*Leptobos syrticus**Miotragocerus cyrenaicus**Redunca* aff. *darti*

?*Hippotragus* sp.  
 cf. *Damalacra* sp.  
*Raphicerus* sp.  
*Gazella* sp.  
*Prostrepsiceros* (*Prostrepsiceros*) *libycus*

### 3. Southwestern and Central Europe

Many localities of mammalian fauna are known from the late Miocene in Southwestern and Central Europe. The following mammalian faunas are represented as Vallesian fauna (Eppelsheim) and Turolian faunas (Dorn-Dürkheim and Mt. Lebéron).

#### (1) Eppelsheim (West Germany)

This fauna is correlated with Vallesian (MN 9). Faunal list of the Eppelsheim Fauna is as follows (Gabuniya, 1959; Klipsten & Kaup, 1836; Wenz, 1921, 1931).

#### Mammalia

##### Primates

*Pliohylobates eppelsheimensis*

##### Rodentia

##### Gliridae

*Steneofiber jägeri*

##### Carnivora

##### Ursidae

*Simocyon diaphorus*

##### Hyaenidae

*Ictitherium robustum*

##### Felidae

*Pontosmilus ogygius*

*Machairodus cultridens*

##### Proboscidea

*Mastodon* (= *Gomphotherium*) *angustidens*

*Mastodon* (= *Gomphotherium*) *angustidens* var. *subtapiroidea*

*Mastodon gigantorostris*

*Mastodon longirostris* var. *dubius*

*Mastodon longirostris* var. *grandis*

##### Deinotheriidae

*Deinotherium giganteus*

##### Perissodactyla

##### Equidae

*Anchitherium* sp.

*Hipparion primigenium*

##### Chalicotheriidae

*Chalicotherium goldfussi*

##### Rhinocerotidae

Aceratheriinae Tribe Aceratherini

*Aceratherium incisivum*

*Brachypotherium goldfussi*

## Rhinocerotinae Tribe Rhinocerotini

*Dicerorhinus schleiermachi**Dicerorhinus belvederensis*

## Artiodactyla

## Suidae

*Sus antiquus**Listriodon* sp.

## Cervidae

*Dorcatherium nauai*

## Flora by Wenz (1921)

*Quercus furcinervus**Quercus undulans**Fagus deukalionis**Fagus castaneaefolia**Laurophyllum crassifolium**Aralites lanceus**Bumelia oreadum*

## Flora by Koenigswald (1929) [palynological]

*Cinnamomum* sp.*Taxodium* sp.*Sequoia* sp.

## (2) Dorn-Dürkheim (West Germany)

This fauna indicates Turolian fauna (MN 11). Faunal list of the Dorn-Dürkheim Fauna is as follows (Tobien, 1980).

## Mammalia

## Rodentia

## Sciuridae

*Spermophilinus* sp.*Pliopetaurista bressana**Pliopetes* sp.*Blackia* sp.*Miopetaurista* sp.

## Castoridae

*Dipoides problematicus**Palaeomys castoroides**Palaeomys plassi* n. sp.*Trogontherium minutum rhenanum* n. sp.*Castor neglectus*

## Cricetidae

*Epimeriones austriacus**Kowalskia* sp. cf. *lavocati**Collimys* sp. cf. *primus**Cricetulodon* sp.

## Anomalomyidae

*Prospalax petteri*

- Pterospalax* sp.
- Muridae
  - Parapodemus lugdunensis*
- Zapodidae
  - Sminthozapus* sp
- Gliridae
  - Muscardinus vireti*
  - Glis* sp. cf. *minor*
  - Microdyromys* sp.
- Carnivora
  - Hyaenidae
    - Percrocuta eximia*
  - Mustelidae
    - Martes* sp. cf. *sansaniensis*
    - Martes* sp.
    - Promeles* sp. D
  - Felidae
    - Pseudaelurus tournauensis*
    - Machairodus taracliensis*
    - Felidarum* inc. subfam.
- Proboscidea
  - Gomphotheriidae
    - Tetralophodon longirostris*
  - Deinotheriidae
    - Deinotherium giganteus*

(3) Mt. Lebéron (France)

This fauna is Turolian fauna (MN 13). Faunal list of the Mt. Lebéron Fauna is as follows (Bernor & Pavlakakis, 1987).

- Mammalia
  - Carnivora
    - Viverridae
      - Herpestes guerini*
    - Hyaenidae
      - Percrocuta eximia*
      - Thalassictis wongii*
      - Plioiviverrops pentelici*
    - Felidae
      - Machairodus aphanistus*
  - Perissodactyla
    - Equidae
      - Hipparion prostylum*
    - Rhinocerotidae
      - Aceratherium* sp.
      - Dicerorhinus schleiermacheri*
  - Artiodactyla

Suidae

*Microstonyx erymanthius*

Cervidae

*Dremotherium* sp.

#### 4. Sub-Paratethys

Many localities of mammalian fauna are known from the late Miocene in Sub-Paratethys. The following mammalian faunas are represented as Turolian faunas (Pikermi, Samos and Maragheh).

##### (1) Pikermi (Greece)

This fauna is famous Turolian fauna (MN 12) of Greece (Wagner 1857; Solounias, 1981). Faunal list of the Pikermi Fauna is as follows (Solounias, 1981).

Mammalia

Insectivora

Talpidae

Uropsilinae

*Desmanella dubia*

Erinaceidae

Gymnurinae

*Galerix atticus*

*Galerix moedlingensis*

Primates

Cercopithecidae

Colobinae

*Mesopithecus pentelici*

Lagomorpha

Ocotonidae

*Proloagus* cf. *crusafonti*

Leporidae

*Alilepus* sp.

Rodentia

Cricetidae

Cricetinae

*Kowalskia* cf. *lavocati*

Cricetodontinae Tribe Cricetodontini

*Byzantinia pikermiensis*

Muridae

Murinae

*Parapodemus gaudryi*

*Occitanomys* ? *neutrum*

*Occitanomys* ? *provocator*

Gliridae

Glirinae

*Muscardinus* sp.

- Myomimus* cf. *dehmi*
- Hystricidae
  - Hystricinae
    - Hystrix primigenia*
- Carnivora
  - Family indet.
    - Simocyon primigenium*
  - Ursidae
    - Indarctos atticus*
  - Mustelidae
    - Mustelinae
      - Sinictis pentelici*
      - Martes woodwardi*
      - ?*Plesiogulo* sp.
    - Melinae
      - Promeles palaeattica*
    - Mephitinae
      - Promephitis lartetii*
    - Lutrinae
      - ?*Enhydriodon laticeps*
  - Hyaenidae
    - Ictitheriinae
      - Plioviverrops orbignyi*
      - Ictitherium viverrinum*
      - Thalassictis hyaenoides*
      - Thalassictis (Lycyaena) chaeretis*
      - Thalassictis (Lycyaena)* sp. nov. (by Solounias 1981)
    - Subfamily indet.
      - Hyaenictis graeca*
      - Hyaenictis eximia*
  - Felidae
    - Felinae
      - Felis* sp.
      - Felis attica*
    - Subfamily indet.
      - Metailurus parvulus*
      - Metailurus major*
    - Machairodontinae
      - Machairodus giganteus*
      - Paramachairodus orientalis*
- Proboscidea
  - Palaeomastodontidae
    - Mammut borsoni* ?
  - Gomphotheriidae
    - Gomphotheriinae
      - Stegotetrabelodon grandincisivus*
      - Choerolophodon pentelici*

## Deinotheriidae

*Deinotherium* cf. *giganteum*

## Hyracoidea

## Procaviidae

*Pliohyrax graecus*

## Perissodactyla

## Equidae

*Hipparion* sp. (large, one preorbital fossa)*Hipparion minus* ? (small, one preorbital fossa)*Hipparion proboscideum* (large, two preorbital fossae)*Hipparion matthewi* (small, no preorbital fossa)

## Chalicotheriidae

*Chalicotherium goldfussi*

## Rhinocerotidae

## Aceratheriinae Tribe Aceratherini

*Aceratherium* cf. *incisivum*

## Rhinocerotinae Tribe Rhinocerotini

*Dicerorhinus schleiermacheri**Dicerorhinus pachygnathus*

## Artiodactyla

## Suidae

*Sus* sp.*Microstonyx erymanthius*

## Cervidae

## Cervinae

Cervinae gen. et sp. indet.

*Pliocervus pentelici*

## Giraffidae

## Palaeotraginae

*Palaeotragus rouenii*

## Sivatheriinae

*Helladotherium duvernoyi*

## Giraffinae

*Honanotherium speciosum**Honanotherium atticum*

## Bovidae

*Miotragocerus-Tragoportax* complex*Miotragocerus monacensis* var. A*Miotragocerus monacensis* var. B*Miotragocerus valenciennesi**Tragoportax amalthea**Tragoportax rugosifrons* ?

## Tribe Antilopini

*Prostrepsiceros rotundicornis* var. A*Protragelaphus skouzesi**Gazella capricornis**Oioceros rothi*



## Tribe Ovibovini

*Palaeoreas lindermayeri**Protoryx* complex*Palaeoryx pallasii* var. A*Palaeoryx pallasii* var. C*Palaeoryx pallasii* var. D*Sporadotragus parvidens**Protoryx carolinae*

## Tribe Tragelaphini

*Selenoportax* sp.

## (2) Samos (Greece)

This fauna is a typical Sub-Paratethys Turolian (MN 12, 13) fauna. Richness of hyaenid, equid and bovid taxa shows an open-country fauna. The bone bearing horizons on Samos Island is comparable to age of between 8.5 and 9.0 Ma by K-Ar dating method (Solounias, 1981). Faunal list of the Samos Fauna is as follows (Solounias, 1981).

## Mammalia

## Insectivora

## Erinaceidae

## Gymnurinae

*Galerix atticus*

## Chiroptera

## Vespertilionidae

## Vespertilioninae

*Samonycteris majori*

## Primates

## Cercopithecidae

## Colobinae

*Mesopithecus pentelici*

## Rodentia

## Sciuridae

*Spermophilinus* cf. *bredai*

## Cricetidae

## Cricetodontinae Tribe Cricetodontini

*Byzantinia hellenicus*

## Gerbillinae

*Pseudomeriones pythagorasi*

## Muridae

## Murinae

*Occitanomys* ? *provocator*

## Spalacinae

*Pliospalax* cf. *sotirisi*

## Hystriidae

## Hystriinae

*Hystrix primigenia*

## Carnivora

## Ursidae

*Ursavus* cf. *depereti**Indarctos atticus*

## Mustelidae

## Melinae

*Promeles palaeattica**Promeles maraghana*

## Mephitinae

*Promephitis lartetii*

## Hyaenidae

## Ictitheriinae

*Plioviverrops orbignyi**Ictitherium viverrinum**Thalassictis wongii**Thalassictis hyaenoides**Thalassictis (Lycyaena) chaeretis**Thalassictis (Lycyaena) sp. nov.* (by Solounias 1981)

## Subfamily indet.

*Hyaenictis eximia*

## Felidae

## Felinae

*Felis attica*

## Subfamily indet.

*Metailurus parvulus**Metailurus major*

## Machairodontinae

*Machairodus giganteus*

## Tubulidentata

## Orycteropodidae

*Orycteropus gaudryi*

## Proboscidea

## Palaeomastodontidae

*Mammot borsoni?*

## Gomphotheriidae

## Gomphotheriinae

*Stegotetralodon grandincisivus**Choerolophodon pentelici*

## Deinotheriidae

*Deinotherium* cf. *giganteum*

## Hyracoidea

## Procaviidae

*Plioxyrax graecus**Plioxyrax kruppii*

## Perissodactyla

## Equidae

*Hipparion* sp. (large, one preorbital fossa)

- Hipparion minus* (small, one preorbital fossa)
- Hipparion proboscideum* (large, two preorbital fossae)
- Hipparion dietrichi* (medium, no preorbital fossa)
- Hipparion matthewi* (small, no preorbital fossa)

Chalicotheriidae

- Ancylotherium pentelicum*

Rhinocerotidae

Aceratheriinae Tribe Aceratherini

- Chilotherium samium*
- Chilotherium schlosseri*
- Chilotherium kowalewski*

Rhinocerotinae Tribe Rhinocerotini

- Dicerorhinus schleiermacheri*
- Dicerorhinus pachygnathus*

Artiodactyla

Suidae

- Microstonyx erymanthius*
- Potamochoerus hytheriordes*

Tragulidae

- Dorcatherium nauai*

Cervidae

Muntiacinae

- Muntiacus* sp.

Cervinae

- Cervinae gen. et sp. indet.
- Pliocervus pentelici*

Giraffidae

Palaeotraginae

- Palaeotragus rouenii*
- Palaeotragus coelophrys*
- Samotherium boissieri*

Sivatheriinae

- Helladotherium duvernoyi*
- Helladotherium* sp. nov. (by Solounias, 1981)

Giraffinae

- Honanotherium speciosum*

Bovidae

*Miotragocerus-Tragoportax* complex

- Miotragocerus monacensis* var. A
- Miotragocerus monacensis* var. B
- Miotragocerus valenciennesi*
- Tragoportax amalthea*
- Tragoportax curvicornis*
- Tragoportax rugosifrons*
- Samokeros minotaurus* var. A
- Samokeros minotaurus* var. B

Tribe Antilopini

- Prostrepsiceros rotundicornis* var. B
- Prostrepsiceros houtumschindleri* var. A
- Protragelaphus skouzesi*
- Gazella capricornis*
- Gazella mytilinii*
- Gazella dorcadooides*
- Oioceros wegneri*
- Sinotragus crassicornis*
- Prosinothragus kuhlmanni*
- Prosinothragus* sp. nov. (by Solounias, 1981)
- Tribe Ovibovini
  - Palaeoreas lindermayeri*
  - Crioetherium argalioides*
  - Parurmiatherium rugosifrons*
- Protoryx* complex
  - Palaeoryx pallasi* var. B
  - Palaeoryx pallasi* var. C
  - Palaeoryx pallasi* var. D
  - Tragoreas oryxoides*
  - Sporadotragus parvidens*
  - Protoryx crassicornis* var. A (long-brained)
  - Protoryx crassicornis* var. B (short-brained)
  - Protoryx laticeps* var. A (long-brained)
  - Protoryx laticeps* var. B (short-brained)
  - Pseudotragus capricornis*
- Tribe Rupicapriini
  - gen. et sp. indet.

### (3) Maragheh (Iran)

This fauna is a typical Turolian fauna of Sub-Paratethys (Mecquenem, 1908-1911, 1924-25; Kamei et al., 1977; Bernor et al., 1980; Solounias, 1981; Bernor, 1986). The Maragheh Formation is comparable to age of between 7 and 11 Ma by K-Ar dating method (Bernor et al., 1980). Faunal list of the Samos Fauna is as follows (Solounias, 1981).

#### Mammalia

##### Primates

##### Cercopithecidae

##### Colobinae

##### *Mesopithecus pentelici*

##### Rodentia

##### Muridae

##### Murinae

##### ?*Gerboa* sp.

##### Carnivora

##### Ursidae

##### *Indarctos atticus*

- Mustelidae
  - Mustelinae
    - Martes* sp.
  - Melinae
    - Promeles palaeattica*
    - Parataxidea maraghana*
    - Parataxidea polaki*
- Hyaenidae
  - Ictitheriinae
    - Thalassictis wongii*
  - Subfamily indet.
    - Hyaenictis eximia*
- Felidae
  - Felinae
    - Felis attica*
  - Subfamily indet.
    - Metailurus parvulus*
  - Machairodontinae
    - Machairodus giganteus*
    - Paramachairodus orientalis*
- Tubulidentata
  - Orycteropodidae
    - Orycteropus gaudryi*
- Proboscidea
  - Gomphotheriidae
    - Gomphotheriinae
      - Choerolophodon pentelici*
- Perissodactyla
  - Equidae
    - Hipparion* sp. (large, one preorbital fossa)
    - Hipparion minus* (small, one preorbital fossa)
    - Hipparion dietrichi* (medium, no preorbital fossa)
  - Chalicotheriidae
    - Ancylotherium pentelicum*
- Rhinocerotidae
  - Aceratheriinae Tribe Aceratherini
    - Chilotherium persiae*
  - Rhinocerotinae Tribe Rhinocerotini
    - Diceros pachygnathus*
  - Rhinocerotinae Tribe Elasmothererini
    - Iranotherium morgani*
- Artiodactyla
  - Suidae
    - Microstonyx erymanthius*
  - Cervidae
    - Cervinae
      - Pliocervus pentelici*

## Giraffidae

## Palaeotraginae

*Palaeotragus coelophrys**Samotherium boissieri*

## Sivatheriinae

*Helladotherium duvernoyi*

## Giraffinae

*Honanotherium atticum*

## Bovidae

*Miotragocerus-Tragoportax* complex*Miotragocerus monacensis* var. B*Samokeros minotaurus* var. A

## Tribe Antilopini

*Prostrepsiceros rotundicornis* var. B*Prostrepsiceros houtumschindleri* var. B*Protragelaphus skouzesi**Gazella deperdita**Oioceros rothi**Oioceros atropatenes**Oioceros rodleri**Sinotragus* sp. nov. (Solounias, 1981)

## Tribe Ovibovini

*Urmitherium polaki**Protoryx* complex*Protoryx crassicornis* var. A (long-brained)*Protoryx crassicornis* var. B (short-brained) ?*Protoryx laticeps* var. A (long-brained)*Protoryx laticeps* var. B (short-brained) ?

## 5. Siwaliks

Many localities of mammalian fauna are known from the late Miocene in Siwaliks. The following mammalian faunas are represented as Astaracian fauna (Chinji), late Vallesian to early Turolian fauna (Nagri) and late Turolian fauna (Dhok Pathan).

## (1) Chinji (Pakistan)

This fauna have none of cervids and Hipparion. Overall faunal resemblances are to Astaracian faunas of Eurasia. An age of between 11 and 13 Ma. Faunal list of the Chinji Fauna is as follows (Pilbeam et al., 1977).

## Mammalia

## Primates

## Hominoidea

*Sivapithecus sivalensis**Sivapithecus indicus**Ramapithecus punjabicus*

## Creodonta

## Hyaenodontidae

*Hyainailouros bugtiensis*

*Dissopsalis carnifex*

Rodentia

Rhizomyidae

cf. Rhizomyidae gen. et sp. indet

Cricetidae

*Copemys* sp.

*Megacricetodon* sp.

Muridae

*Antemus chinjiensis*

Carnivora

Amphicyonidae

Amphicyoninae (large sp.)

*Amphicyon* sp.

*Vishnucyon chinjiensis*

Mustelidae

*Martes lydekkeri*

?*Martes* sp.

*Vishnuonyx chinjiensis*

Mustelinae sp.

Viverridae

?*Viverra chinjiensis*

Hyaenidae

Hyaenidae gen. et sp. indet.

*Percrocuta carnifex*

Felidae

'*Sivasmilus*' (= *Paramachairodus copei* )

*Sivaelurus chinjiensis*

Felidae gen. et sp. indet.

?*Sansanosmilus* sp.

Tubulidentata

Orycteropodidae

*Orycteropus* sp.

Perissodactyla

Chalicotheriidae

*Chalicotherium salinum*

Rhinocerotidae

Rhinocerotidae spp.

Artiodactyla

Suidae

*Listriodon pentapotamiae*

*Conohyus chinjiensis*

*Lophochoerus* sp.

*Merycopotamus pusillus*

*Dorcabune nagrii*

Tragulidae

Tragulidae spp.

## Giraffidae

*Giraffokeryx* sp.

## Bovidae

*Protragocerus gluten**Miotragocerus gradiens**Kubanotragus sokolovi**?Pseudotragus potwaricus**Sivoreas eremita**Gazella* sp.

## (2) Nagri (Pakistan)

The bovids, suids, rodents and the two species of Hipparion of this fauna suggest a correlation with late Vallesian or early Turolian faunas. Upper half of Nagri Formation is probably comparable to age of between 9 and 10 Ma with age of Samos and Turkish faunas. The lower half of Nagri Formation suggests earlier Vallesian. Faunal list of the Nagri Fauna is as follows (Pilbeam et al., 1977).

## Mammalia

## Insectivora

## Soricidae

gen. et sp. indet.

## Primates

*?Lorisidae*

gen. et sp. indet.

## Hominoidea

*Sivapithecus sivalensis**Sivapithecus indicus**Ramapithecus punjabicus*cf. *Gigantopithecus* sp.

## Rodentia

## Sciuridae

gen. et sp. indet.

## Gliridae

gen. et sp. indet.

## Rhizomyidae

*Rhizomyoides* sp.*Kanisamys sivalensis*

## Muridae

*Progonomys* n. sp.*Parapodemus* sp.cf. "*Mastomys*" *colberti*

## Creodonta

## Hyaenodontidae

cf. *Isohyaenodon* sp.

## Carnivora

## Amphicyonidae

*Amphicyon* sp.



## Mustelidae

?*Martes* sp.

Mustelinae sp.

*Eomellivora* sp.

*Sivaonyx bathygnathus*

## Viverridae

Viverrinae 2 sp.

?Herpestinae sp.

?*Progenetta* sp.

## Hyaenidae

*Palyhyaena sivalensis*

?*Miohyaena* n. sp.

*Percrocuta carnifex*

*Percrocuta grandis*

## Felidae

? *Sivaelurus* sp.

Machairodontinae

## Proboscidea

## Gomphotheriidae

gen. et sp. indet.

## Deinotheriidae

*Deinotherium* sp.

## Perissodactyla

## Equidae

*Hipparion* small and large spp.

## Chalicotheriidae

*Chalicotherium* cf. *salinum*

## Artiodactyla

## Suidae

*Propotamochoerus hysudricus*

*Propotamochoerus* sp.

*Conotylus* sp.

*Tetraconodon* sp.

*Hippopotamodon sivalense* (= *Dicryphochoerus titan*)

## Tayassuidae

*Schizochocerus* sp.

## Anthracotheriidae

*Merycopotamus namus*

*Merycopotamus dissimilis*

## Tragulidae

*Dorcabune nagrii*

*Dorcatherium majus*

*Dorcatherium minus*

cf. *Dorcatherium* sp.

## Giraffidae

cf. *Sivatherium* sp.

## Bovidae

*Gazella* sp.

*Miotragocerus punjabicus*

*Selenoportax vexillarius*

?*Pseudotragus* sp.

Boselaphini very small gen. et sp. nov.

### (3) Dhok Pathan (Pakistan)

The Dhok Pathan fauna resembles those from late Turolian in Eurasia and North Africa. The Dhok Pathan Formation is probably comparable in age of between 8 and 9 Ma (or perhaps less) with age of Samos and Turkish faunas. Faunal list of the Dhok Pathan Fauna is as follows (Colbert, 1935; Pilbeam et al., 1977).

#### Mammalia

##### Primates

###### Cercopithecidae

*Cercopithecus hasnoti*

*Macaca sivalensis*

###### Hominioidea

*Dryopithecus frickae*

#### Rodentia

##### Rhizomyidae

*Rhizomyoides* sp.

*Kanisamys sivalensis*

##### Hystriidae

*Hystrix sivalensis*

#### Carnivora

##### Amphicyonidae

*Amphicyon lydekkeri*

##### Ursidae

*Agriotherium palaeindicum*

*Indarctos salmontanus*

*Indarctos punjabiensis*

##### Mustelidae

?*Martes* sp.

Mustelinae sp.

*Eomellivora* sp.

*Sivaonyx bathygnathus*

##### Viverridae

Viverrinae 2 sp.

?*Herpestinae* sp.

?*Progenetta* sp.

##### Hyaenidae

*Palyhyaena sivalensis*

?*Miohyaena* n. sp.

*Percrocuta carnifex*

*Percrocuta grandis*

- Felidae
  - ? *Sivaelurus* sp.
- Machairodontinae
- Proboscidea
  - Gomphotheriidae
    - gen. et sp. indet.
  - Deinotheriidae
    - Deinotherium* sp.
- Perissodactyla
  - Equidae
    - Hipparion* small and large spp.
  - Chalicotheriidae
    - Chalicotherium* cf. *salinum*
- Artiodactyla
  - Suidae
    - Propotamochoerus hysudricus*
    - Propotamochoerus* sp.
    - Conotylus* sp.
    - Tetraconodon* sp.
    - Hippopotamodon sivalense* (= *Dicryphochoerus titan*)
  - Tayassuidae
    - Schizochocerus* sp.
  - Anthracotheriidae
    - Merycopotamus namus*
    - Merycopotamus dissimilis*
  - Tragulidae
    - Dorcabune nagrii*
    - Dorcatherium majus*
    - Dorcatherium minus*
    - cf. *Dorcatherium* sp.
  - Giraffidae
    - cf. *Sivatherium* sp.
  - Bovidae
    - Gazella* sp.
    - Miotragocerus punjabicus*
    - Selenoportax vexillarius*
    - ?*Pseudotragus* sp.
    - Boselaphini very small gen. et sp. nov.

## 6. China

Many localities of mammalian fauna are known from the late Miocene in China. The following mammalian faunas are represented as early Turolian fauna (Baode) and late Turolian fauna (Yushe I).

### (1) Baode, Shanxi

This fauna is correlated with early Turolian mammalian age of West Eurasia and richness of hyaenid, equid and bovid taxa indicate open-country environments. Faunal

list of the Baode Fauna is as follows (Yen et al. eds., 1984; Qiu et al., 1987).

Mammalia

Rodentia

Castoridae

*Sinocastor zdanskyi*

Carnivora

Amphicyonidae

*Amphicyon* sp.

Ursidae

*Sinocyon* cf. *primigenium*

*Indarctos lagrelii*

*I. sinensis*

Mustelidae

*Eomellivora wimani*

*Lutra aonychoides*

*Martes palaeosinensis*

*Melodon incertum*

*Melodon major*

*Parataxidea crassa*

*Parataxidea sinensis*

*Plesiogulo brachygnathus*

*Proputorius minimus*

*Sinictis dolichognathus*

Hyaenidae

*Hyaena honanensis*

*Hyaena variabilis*

*Ictitherium gaudryi*

*Ictitherium hyaenoides*

*Ictitherium sinensis*

*Ictitherium wongi*

*Lycyaena dubia*

Felidae

*Homotherium palanderi*

*Homotherium tingi*

*Pseudaelurus major*

*Pseudaelurus minor*

Proboscidea

Gomphotheriidae

*Tetralophodon exoletus*

Perissodactyla

Equidae

Hipparioninae

*Hipparion* (*Hipparion*) *dermatorhinum*

*Hipparion* (*Hipparion*) *fossatum*

*Hipparion* (*Hipparion*) *hippidodus*

*Hipparion* (*Hipparion*) *placodus*

- Anchitheriinae
  - Sinohippus ziteli*
- Rhinocerotidae
  - Aceratheriinae
    - Chilotherium anderssoni*
    - Chilotherium gracile*
    - Chilotherium habereri*
    - Chilotherium planifrons*
    - Chilotherium samium*
    - Chilotherium schlosseri*
    - Chilotherium wimani*
  - Rhinocerotinae
    - Dicerorhinus orientalis*
  - Iranotheriinae (Elasmotheriinae)
    - Sinootherium lagrelii*
- Artiodactyla
  - Suidae
    - Chleuastochoerus stehlini*
    - Potamochoerus hytheriordes*
    - Sus erymanthius*
  - Cervidae
    - Cervavitus novorossiae*
    - Procapreolus latifrons*
  - Giraffidae
    - Palaeotragus* cf. *coelophrys*
    - Palaeotragus microdon*
    - Samotherium sinense*
  - Bovidae
    - Paraprotoryx minor*
    - Miotragocerus-Tragoportax* complex
    - Tragocerus gregarius*
    - Tragocerus lagrelii*
    - Tragocerus spectabilis*
    - Gazella altidens*
    - Gazella dorcadoides*
    - Gazella gaudryi*
    - Gazella paotehensis*
    - Sinotragus wimani*
    - Plesiadax depereti*
    - Plesiadax minor*
    - Urmitherium intermedium*
    - Protoryx shansiensis*

(2) Yushe Zone I, Shanxi

This fauna is correlated with late Turolian mammalian age of West Eurasia and indicates woodland environments. Faunal list of the Yushe Zone I Fauna is as follows (Yen et al. eds., 1984; Qiu et al., 1987).

## Mammalia

## Rodentia

## Castoridae

*Sinocastor zdanskyi*

## Cricetidae

*Prosiphneus murinus*

## Carnivora

## Ursidae

*Sinocyon cf. primigenium**Hyaenarctis* sp.

## Mustelidae

*Lutra aonychoides**Martes palaeosinensis**Plesiogulo brachygnathus*

## Hyaenidae

*Ictitherium gaudryi*

## Felidae

*Homotherium palanderi**Pseudaelurus major**Pseudaelurus minor**Felis* sp.

## Proboscidea

## Gomphotheriidae

*Gomphotherium wimani**Tetralophodon exoletus**Tetralophodon* sp.*Anancus cuneatus**Anancus sinensis**Selenolophodon spectabilis*

## Stegodontidae

*Stegodon yushensis*

## Perissodactyla

## Equidae

## Hipparioninae

*Hipparion (Hipparion) platyodus*

## Tapiridae

*Tapirus teilhardi*

## Rhinocerotidae

## Rhinocerotinae

*Dicerorhinus orientalis**"Dicerorhinus palaeosinensis"*

## Artiodactyla

## Suidae

*Chleuastochoerus stehlini**Sus erymanthius*

## Cervidae

*Axis speciosus*  
*Eostyloceros blainvillei*  
*Eostyloceros triangularis*  
*Procapreolus latifrons*  
*Cervavitus demissus*  
*Cervavitus novorossiae*  
*Procapreolus latifrons*

Giraffidae

*Palaeotragus decipens*  
*Palaeotragus* sp.  
*Honanotherium schlosseri*

Bovidae

*Dorcadoryx triguetricornis*  
*Paraprotoryx killgusi*  
*Sinoryx bombifrons*  
*Tragocerus laticornis*  
*Gazella gaudryi*  
*Oioceros* sp.  
*Protoryx bohlini*  
*Protoryx yushensis*  
*Tragoreas palaeosinensis*

In the discussion section, The author analyses faunal resemblance from the evidence of well over 500 taxa of 22 Eurasian faunas shown in Appendix 1 (p. 103–112).

#### IV. Neogene Faunal Aspects and Paleocology of Sub-Saharan Africa

The geographical distribution and paleocology of Sub-Saharan faunas in each age is remarked in the following chapter (Fig. 9).

The following zonation of Sub-Saharan Africa is based largely on the radiometric age and faunal resemblance (Benefit & Pickford, 1986; Nakaya, 1987, 1989, 1993; Nakaya et al., in press; Pickford, 1981, 1982, 1986a, 1986b; this work). East African mammalian faunas are described in the following chapter (p. 50–75) in detail.

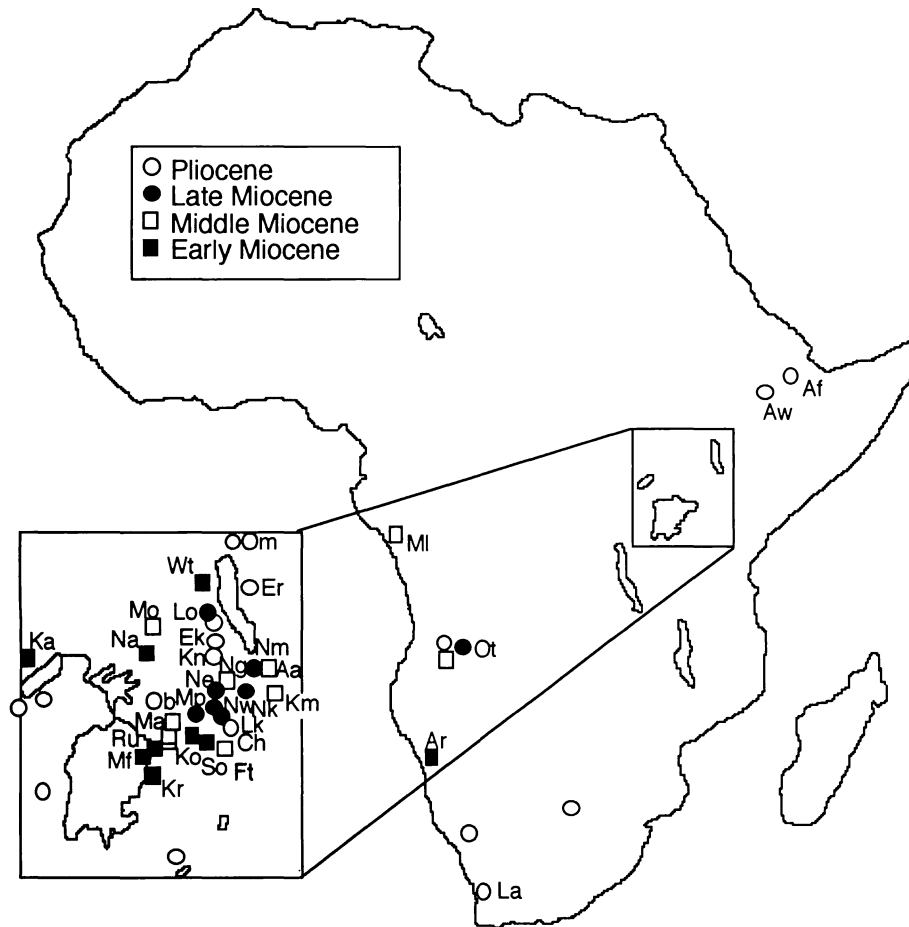
##### 1. Miocene

###### (1) Agenian

The following Agenian (18–22 Ma) mammalian faunas are sporadically distributed in South Africa, Zaire and East Africa. Correlation of the Faunal Sets of East Africa is followed after Pickford (1981).

Pre Set I (early Agenian); Meswa (Kenya).

Set I (late Agenian); Malembe (Zaire: Hooijer, 1963, 1970), Napak (Uganda), Koru (Kenya), Songhor (Kenya), Kiahera (Kenya), Chemtwara (Kenya).



**Fig. 9.** Neogene vertebrate localities from the Sub-Saharan Africa.

Aa: Aka Aiteputh; Af: Afar; Ar: Arrisdraft; Aw: Middle Awash; Ch: Chemeron; Ek: Ekora; Er: East Rudolf; Ft: Fort Ternan; Ka: Karugamania; Km: Kirimun; Kn: Kanapoi; Ko: Koru; Kr: Karungu; La: Langebaanweg; Lk: Lukeino; Lo: Lothagam; Na: Napak; Ne: Ngorora E; Ng: Ngorora; Nk: Nakali; Nm: Namurungule; Nw: Ngeringerowa; Ma: Maboko; Mp: Mfwangano; Mi: Malembe; Mo: Moroto; Mp: Mpesida; Ob: Ombo; Om: Omo; Ru: Rusinga; Ot: Otavi; So: Songhor; Wt: West Turkana.

## (2) Orlanian

The following Orlanian (15-18 Ma) mammalian faunas are sporadically distributed in South Africa and East Africa. Correlation of the Faunal Sets of East Africa is followed after Pickford (1981). Some fauna are characterized by dominant Primates (Maboko Fauna).

Set II (early Orlanian); Hiwegi, Gumbo, Chianda (Rusinga Island, Kenya), Bukwa (Kenya), Moruorot (Kenya), Karungu (Kenya), Mfwangano (Kenya).



Set III (late Orleanian); Arrisdrift (Namibia; South West Africa early middle Miocene 14-18 Ma; Hende, 1978), Ombo (Kenya), Maboko (Kenya), Buluk (Kenya), Loperot (Kenya), Kirimun (Kenya), Majiwa (Kenya).

### (3) Astaracian

The following Astaracian (12.5-15 Ma) mammalian faunas are sporadically distributed in East Africa only. Correlation of the Faunal Sets of East Africa is followed after Pickford (1981). Some fauna are characterized by dominant Primates (Aka Aiteputh Fauna).

Set IV (Astaracian); Moroto (Uganda), Aka Aiteputh (Kenya), Fort Ternan (Kenya), Muryur (Kenya), Otavi BA-1, 47, 63, (Namibia: Conroy et al., 1992).

### (4) Vallesian

The Vallesian (10.5-12.5 Ma) mammalian faunas are distributed in East Africa only. Hipparion appeared about 12.5 Ma in Sub-Saharan Africa. The Ngorora Fauna has rich assemblage.

Set V (Vallesian); Ngorora (Kenya), Otavi BA-31, 90 (Namibia: Conroy et al., 1992).

### (5) Turolian

The following Turolian (5.5-10.5 Ma) mammalian faunas are sporadically distributed in East Africa only. This fauna is considered as a core of the Sub-Saharan mammalian faunas after Miocene. The mammalian assemblage of Sub-Saharan African faunas changed since late Astaracian. Some recent genera of mammals appeared in East Africa, in post-Vallesian age. Therefore, the Namurungule Fauna is very important, from the viewpoint of the process of the environmental change during the late Miocene and the effects of this paleoenvironmental change to the Hominoid evolution. Table 3 shows a list of taxa of the Ngorora Fauna of the Vallesian, the Nakali, Ngeringerowa, Ngorora E Formation (Benefit & Pickford, 1986) and Namurungule Fauna (Nakaya et al., in press; Kawamura & Nakaya, in press) of the Turolian East Africa. The Namurungule Fauna has rich assemblage among the Turolian faunas, however, other faunas have poor assemblage.

Set VI (early Turolian); Ngorora upper E (Kenya), Ngeringerowa (Kenya), Nakali (Kenya), Namurungule (Kenya).

Set VII (late Turolian); Mpesida (Kenya), Lukeino (Kenya) and Lothagam I (Kenya).

## 2. Pliocene

### (1) Ruscinian

The following Ruscinian (3.5-5.5 Ma) mammalian faunas are distributed in East Africa and South Africa. The first family Hominidae (*Australopithecus*) appeared in these faunas.

Set VIII (Ruscinian); Afar (Ethiopia), Middle Awash (Ethiopia), Chemeron (Kenya), Ekora (Kenya), Kanapoi (Kenya), Lothagam (Kenya), Laetoli (Tanzania), Otavi BA-8, 54 (Namibia: Conroy et al., 1992), Langebaanweg (South Africa).

**Table 3.** A list of taxa of each fauna of the Vallesian to early Turolian mammalian faunas of East Africa.

Taxa / Locality	NM	NG	NE	NK	NW
Hominoidea small form		1			
Hominoidea large form	1	1			
Cercopithecoidea indet.		1			
Colobinae sp.				1	
<i>Microcolobus tugenensis</i>					1
<i>Agnotherium</i> sp.		1			
<i>Eomellivora</i> sp.		1			
<i>Sivaonyx</i> sp.		1			
Hyaenidae ( <i>Percrocuta</i> sp.)	1	1			
Canidae small sp.		1			
<i>Orycteropus chemeldoi</i>	?	1			
<i>Choerolophodon ngorora</i>		1	1	?	
<i>Tetralophodon</i> sp.	1	1			
<i>Deinotherium</i> sp. cf. <i>bozasi</i>	1	1		1	1
<i>Paraplioxyrax</i> sp.		1	1		
<i>Hipparion</i> large form	1		1	1	1
<i>Hipparion</i> small form	1				
<i>Ancylotherium</i> sp. ?	1				
<i>Aceratherium/Dicerorhinus</i> sp.		1			
<i>Chilotheridium pattersoni</i>	1	1			
<i>Paradiceros</i> sp.	1				
<i>Brachypotherium lewisi</i>		1			
<i>Kenyatherium bishopi</i>	1			1	
? <i>Conohyus</i> sp.		1			
<i>Lopholistriodon kidogosana</i>		1			
<i>Nyanzachoerus</i> sp.	1		1	1	
Tayassuidae		1			
<i>Kenyapotamus coryndoni</i>	1	1	1		1
<i>Kenyapotamus</i> sp.				1	
<i>Dorcatherium pigotti</i>		1			1
<i>Palaeotragus</i> sp.	1	1	1	?	1
Giraffidae large form ( <i>Samotherium</i> sp.)	1	1			
<i>Climacoceras gentryi</i>		1			
<i>Protragocerus labidotus</i>		1			
<i>Sivoreas/Palaeoreas</i> sp.	1	1			1
Hippotraginae/Reduncini				1	1
<i>Homoiodorcas tugenium</i>		1			
? <i>Antidorcas</i> sp.		1			1
<i>Pseudotragus? gentryi</i>		1	1		
<i>Pachytragus</i> sp.	1	1			
<i>Gazella</i> sp.	1				
<i>Paraphiomys pigotti</i>	1				
<i>Paraulacodus</i> sp.	1				

Note: NG: Ngorora A-D; NE: Ngorora Upper E; NK: Nakali; NW: Ngeringerowa (Benefit & Pickford, 1986); NM: Namurungule (Nakaya et al., in press; Kawamura & Nakaya., in press).

## V. Development of Neogene Mammals in East Africa

The age of some Neogene mammalian sites from East Africa has been determined by radiometric dating methods. The age of many sites were determined by stratigraphical correlation and faunal resemblance. The following description shows mammalian assemblages, age (radiometric and so on), and paleoenvironment at each location (country).

### (1) Meswa (Kenya)

The age of this fauna was determined as Faunal Set Pre-Set I by faunal assemblages and this fauna must have inhabited in subaerial environments deduced from sedimentological evidence (Andrews et al., 1981; Pickford, 1986a). Faunal list of the Meswa Fauna is following Pickford (1986a).

Mammalia

Primates

Oreopithecidae gen. nov.

Artiodactyla

*Walangania africanus*

### (2) Napak (Uganda)

The age of this fauna was determined as 19-25 Ma by K-Ar dating and as Faunal Set I by faunal assemblages and this fauna must have inhabited in subaerial environments deduced from sedimentological evidence (Bishop, 1962, 1967; Pickford, 1981). Faunal list of the Napak Fauna is as follows (Bishop, 1962, 1967).

Mammalia

Insectivora

*Miohyncocyon clarki*

*Myohyrax oswaldi*

*Hiwagicyon juvenalis*

*Parageogale aletris*

*Protenrec tricuspis*

*Gymnuechinus leakeyi*

*Gymnuechinus camptolophus*

*Amphuechinus rusingensis*

*Galerix africanus*

*Propotto leakeyi*

Molossidae sp. nov.

Emballonuridae gen. et sp. indet.

Megalodermatidae gen. et sp. indet.

*Komba minor*

*Komba robustus*

Primates

*Progalago songhorensis*

*Mioeoticus* sp.

*Dendropithecus macinnesi*

*Limnopithecus legetet*  
*Proconsul africanus*  
*Proconsul nyanzae*  
*Rangwapithecus gordoni*  
*Nyanzapithecus vancouveringi*

## Rodentia

*Kenyalagomys rusingae*  
*Kenyalagomys minor*  
*Paraphiomys pigotti*  
*Paraphiomys stromeri*  
*Epiphomys coryndoni*  
*Elimerimys woodi*  
*Diamantomys leuderitzi*  
*Kenyamys mariae*  
*Simonimys genovefae*  
*Myophiomys arambourgi*  
*Ploheliophobius leakeyi*  
*Paranomalurus soniae*  
*Paranomalurus walkeri*  
*Megapedetes pentadactylus*  
Pedetidae gen. et sp. nov.  
*Protarsomys macinnesi*  
*Vulcanisciurus africanus*  
*Teratodon enigmae*  
*Pterodon nyanzae*  
*Anasinopa leakeyi*  
*Metapterodon kaiseri*

## Creodonta

*Leakeytherium hiwegi*  
*Hyaenodon andrewsi*  
*Hyaenodon pilgrimi*  
*Hecubides euryodon*  
*Hecubides macrodon*  
*Kichechia zamanae*  
*Afrosmilus africanus*

## Tubulidentata

*Myorycteropus africanus*

## Proboscidea

*Prodeinotherium hobleyi*  
*Archaeobelodon* sp.  
*Eozygodon morotoensis*

## Hyracoidea

*Pachyhyrax championi*  
*Prohyrax bateae*

## Perissodactyla

*Chalicotherium rusingense*  
*Dicerorhinus leakeyi*

*Aceratherium acutirostratum*

*Brachypotherium heinzlini*

Artiodactyla

*Hyoboaops africanus*

*Masritherium aequitoralis*

*Diamantohyus africanus*

*Libycochoerus jeanelli*

*Kenyasus rusingensis*

*Nguruwa kijivium*

*Dorcatherium chappuisi*

*Dorcatherium pigotti*

*Dorcatherium parvum*

*Canthumeryx sirtensis*

*Propalaeoryx nyanzae*

*Walangania africanus*

(3) Koru (Kenya)

The age of this fauna was determined as Faunal Set I by faunal assemblages and this fauna must have inhabited in subaerial, apron of central volcano, and intermittent deposition with pedogenesis environments deduced from sedimentological evidence (Bishop, 1967; Pickford, 1981, 1986a). Faunal list of the Koru Fauna is as follows (Bishop, 1967).

Mammalia

Insectivora

*Amphechinus rusingensis*

*Erythrozoetes chamerpes*

*Prochrysochloris miocaenicus*

*Rhynchocyon clarki*

*Saccolaimus incognita*

Primates

*Progalago* sp.

*Limnopithecus legetet*

*Proconsul africanus*

*Proconsul nyanzae*

Rodentia

*Teratodon spekei*

*Hecubides euryodon*

Proboscidea

*Deinotherium* sp.

Perissodactyla

*Chalicotherium rusingense*

Artiodactyla

*Dorcatherium songhorensis*

*Palaeomeryx africanus*

(4) Songhor (Kenya)

The age of this fauna was determined as Faunal Set I by faunal assemblages and this

fauna must have inhabited in subaerial, apron of central volcano, intermittent deposition with pedogenesis environments deduced from sedimentological evidence (Bishop, 1967; Pickford, 1981, 1986a). Faunal list of the Songhor Fauna is as follows (Bishop, 1967).

#### Mammalia

##### Insectivora

*Rhynchocyon clarki*  
*Rhynchocyon rusingae*  
*Protenrec tricuspis*  
*Gymnuechinus songhorensis*  
*Amphechinus rusingensis*  
*Galerix africanus*  
*Prochrysochloris miocaenicus*

##### Primates

*Progalago dorae*  
*Progalago robustus*  
*Progalago minor*  
*Limnopithecus legetet*  
*Limnopithecus macinnesi*  
*Proconsul africanus*  
*Proconsul nyanzae*  
*Proconsul major*

##### Rodentia

*Paraphiomys pigotti*  
*Paraphiomys* small form  
*Diamantomys* sp.  
*Megapedetes pentadactylus*  
Pedetidae small form  
*Teratodon enigmae*  
*Teratodon spekei*  
*Bathyergoides* sp.  
*Cricetodon* sp.  
Anomaluridae large form  
Anomaluridae small form

##### Creodonta

*Hyaenodon andrewsi*  
*Hyaenodon pilgrimi*  
*Hecubides matthewi*  
*Kichechia zamanae*

##### Carnivora

*Metailurus africanus*  
*Hyootherium* sp.

##### Hyracoidea

*Megalohyrax championi*  
*Myohyrax* sp.  
*Bunohyrax* sp.

## Proboscidea

*Gomphotherium* sp.

## Perissodactyla

*Chalicotherium rusingense*

## Artiodactyla

*Dorcatherium songhorensis**Palaeomeryx africanus*

## (5) Rusinga (Kenya)

The mean age of Rusinga Group was determined as 17.9 Ma (Hiwegi Formation: 16.9-34.5 Ma, Rusinga Agglomerate: 16.6-21.9 Ma, Kiahera Formation: 17.2-22.9 Ma) by K-Ar dating (Drake et al., 1988) and as Faunal Set II by faunal assemblages (Pickford, 1981). Faunal list of the Songhor Fauna is as follows (Drake et al., 1988).

## Mammalia

## Insectivora

*Miohyncocyon clarki**Myohyrax oswaldi**Hiwagicyon juvenalis**Parageogale aletris**Protenrec tricuspis**Gymnuechinus leakeyi**Gymnuechinus camptolophus**Amphuechinus rusingensis**Galerix africanus**Propotto leakeyi*

Molossidae sp. nov.

Emballonuridae gen. et sp. indet.

Megalodermatidae gen. et sp. indet.

*Komba minor**Komba robustus*

## Primates

*Progalago songhorensis**Mioeuoticus* sp.*Dendropithecus macinnesi**Limnopithecus legetet**Proconsul africanus**Proconsul nyanzae**Rangwapithecus gordonii**Nyanzapithecus vancouveringi*

## Rodentia

*Kenyalagomys rusingae**Kenyalagomys minor**Paraphiomys pigotti**Paraphiomys stromeri**Epiphomys coryndoni**Elimerimys woodi*

*Diamantomys leuderitzi*  
*Kenyamys mariae*  
*Simonimys genovefae*  
*Myophiomys arambourgi*  
*Ploheliophobius leakeyi*  
*Paranomalurus soniae*  
*Paranomalurus walkeri*  
*Megapedetes pentadactylus*  
Pedetidae gen. et sp. nov.  
*Protarsomys macinnesi*  
*Vulcanisciurus africanus*  
*Teratodon enigmae*  
*Pterodon nyanzae*  
*Anasinopa leakeyi*  
*Metapterodon kaiseri*  
*Leakeytherium hiwegi*  
*Hyaenodon andrewsi*  
*Hyaenodon pilgrimi*  
*Hecubides euryodon*  
*Hecubides macrodon*  
*Kichechia zamanae*

## Carnivora

*Afrosmilus africanus*

## Tubulidentata

*Myorycteropus africanus*

## Proboscidea

*Prodeinotherium hobleyi*  
*Archaeobelodon* sp.  
*Eozygodon morotoensis*

## Hyracoidea

*Pachyhyrax championi*  
*Prohyrax bateae*

## Perissodactyla

*Chalicotherium rusingense*  
*Dicerorhinus leakeyi*  
*Aceratherium acutirostratum*  
*Brachypotherium heinzlini*

## Artiodactyla

*Hyoboops africanus*  
*Masriitherium aequitoralis*  
*Diamantohyus africanus*  
*Libycochoerus jeanelli*  
*Kenyasus rusingensis*  
*Nguruwa kijivium*  
*Dorcatherium chappuisi*  
*Dorcatherium pigotti*  
*Dorcatherium parvum*



*Canthumeryx sirtensis*

*Propalaeoryx nyanzae*

*Walangania africanus*

#### (6) Karungu (Kenya)

The age of this fauna was determined as 17.5-17.7 Ma by K-Ar dating (Drake et al., 1988) and as Faunal Set II by faunal assemblages (Pickford, 1981). This fauna must have inhabited in lacustrine, lake margin and swamp, wet part of flood plain and large river system in volcanic arena deduced from sedimentological evidence (Pickford, 1981). Faunal list of the Karungu Fauna is as follows (Drake et al., 1988).

#### Mammalia

##### Primates

*Dendropithecus macinnesi*

*Proconsul nyanzae*

##### Rodentia

? *Kenyalagomys rusingae*

*Paraphiomys pigotti*

*Paraphiomys stromeri*

*Diamantomys leuderitzi*

*Anasinopa leakeyi*

*Metapterodon kaiseri*

? *Kichechia zamanae*

##### Carnivora

*Afromsmlus africanus*

##### Tubulidentata

*Myorycteropus africanus*

*Orycteropus minutus*

##### Proboscidea

*Prodeinotherium hobleiy*

*Archaeobelodon* sp.

##### Hyracoidea

*Myohyrax oswaldi*

*Pachyhyrax championi*

? *Prohyrax bateae*

##### Perissodactyla

*Chalicotherium rusingense*

*Dicerorhinus leakeyi*

*Aceratherium acutirostratum*

*Brachypotherium heinzlini*

##### Artiodactyla

*Hyoboops africanus*

*Masritherium aequitoralis*

*Diamantohyus africanus*

*Libycochoerus jeanelli*

*Kenyasus rusingensis*

*Dorcatherium chappuisi*

*Dorcatherium parvum*  
 ? *Canthumeryx sirtensis*  
*Propalaeoryx nyanzae*  
*Walangania africanus*

(7) Mfwangano (Kenya)

The age of this fauna was determined as 21.7 Ma (Kiahera Formation) by K-Ar dating (Drake et al., 1988). This fauna must have inhabited in subaerial, apron of central volcano, intermittent deposition with pedogenesis, and dry part of floodplain in volcanic arena deduced from sedimentological evidence (Pickford, 1981). Faunal list of the Kiahera Formation of the Mfwangano Fauna is as follows (Drake et al., 1988).

Mammalia

*Myohyrax oswaldi*  
*Komba robustus*

Primates

*Dendropithecus macinnesi*  
*Proconsul africanus*  
*Proconsul nyanzae*

Rodentia

*Kenyalagomys rusingae*  
*Paraphiomys pigotti*  
*Paraphiomys stromeri*  
*Diamantomys leuderitzi*  
*Megapedetes pentadactylus*  
*Hecubides euryodon*

Proboscidea

*Prodeinotherium hobleyi*

Hyracoidea

? *Pachyhyrax championi*

Perissodactyla

*Brachypotherium heinzlini*

Artiodactyla

*Masritherium aequitoralis*  
*Kenyasus rusingensis*  
*Nguruwa kijivium*  
*Dorcatherium pigotti*  
*Propalaeoryx nyanzae*  
*Walangania africanus*

(8) Buluk (Kenya)

The age of this fauna was determined as 17.3 Ma by K-Ar dating and as Faunal Set III by faunal assemblages. This fauna must have inhabited in a shallow or intermittent aquatic environments and intertributary or behind-shore lagoon facies deduced from sedimentological evidence (Harris & Watkins, 1974; Pickford, 1981). Faunal list of the Buluk Fauna is as follows (Harris & Watkins, 1974).

## Reptilia

## Crocodylia

## Crocodylidae

gen. et sp. indet.

## Testudines

gen. et sp. indet.

## Mammalia

## Creodonta

gen. et sp. indet.

## Proboscidea

*Platybelodon kisumuensis**Prodeinotherium hobleyi*

## Hyracoidea

*Megalohyrax championi*

## Perissodactyla

*Dicerorhinus* sp.

## Artiodactyla

*Listriodon* sp.

## (9) Kiriun (Kenya)

The age of this fauna was determined as 11.5-15Ma by K-Ar and fission track dating and as Faunal Set III by faunal assemblages (Pickford, 1981). Sanithere and tragulid (Artiodactyla) indicates woodland environments (Kawamura & Nakaya, 1982; Pickford 1982; Matsuda et al., 1986). Faunal list of the Kiriun Fauna is as follows (Kawamura & Nakaya, 1982; Pickford, 1982).

## Mollusca

## Gastropoda

## Ampullariidae

*Saulea lithoides*

## Cyclophoridae

*Maizania lugubrioides*

## Pomatiasidae

*Ligatella* sp.

## Enidae

? *Edouardia* sp.

## Achtinidae

*Burtoa* cf. *nilotica**Limicolaria* sp.

## Pisces

fam., gen. et sp. indet.

## Reptilia

## Crocodylia

## Crocodylidae

gen. et sp. indet.

## Testudines

## Testudinidae

- gen. et sp. indet.
- Pelomedusidae
- gen. et sp. indet.
- Mammalia
- Rodentia
- Thryonomyidae
- Paraphiomys* cf. *pigotti*
- Paraphiomys* sp.
- Pedetidae
- ? *Megapedetes* sp.
- Cricetodontidae
- Afrocricetodon* sp.
- Carnivora
- fam., gen. et sp. indet.
- Proboscidea
- Gomphotheriidae
- gen. et sp. indet.
- Deinotheriidae
- ? *Prodeinotherium* sp.
- Hyracoidea
- Procaviidae
- gen. et sp. indet.
- Perissodactyla
- Rhinocerotidae
- Brachypotherium heinzeli*
- Artiodactyla
- Sanitheriidae
- Sanitherium* sp.
- Tragulidae
- Dorcatherium* cf. *pigotti*
- Dorcatherium* sp.

#### (10) Ombo (Kenya)

The age of this fauna was determined as Faunal Set III by faunal assemblages and this fauna must have inhabited in lake margin, swamp, large river system in volcanic arena deduced from sedimentological evidence (Bishop, 1967; Pickford, 1981). Faunal list of the Ombo Fauna is as follows (Bishop, 1967).

- Mammalia
- Primates
- ? *Mesopithecus* sp.
- Creodonta
- Hyaenodon* sp.
- Hyaenodon andrewsi*
- Pterodon nyanzae*
- Hyoboops (Merycops) africanus*
- Proboscidea

*Gomphotherium* sp.

*Deinotherium* sp.

Perissodactyla

Rhinocerotidae

Artiodactyla

Suidae

*Dorcatherium pigotti*

Tragulidae

#### (11) Maboko (Kenya)

The age of this fauna was determined as 12.5 Ma by K-Ar dating and as Faunal Set III by faunal assemblages (Pickford, 1981). This fauna must have inhabited in dry and wet part of floodplain in volcanic arena deduced from sedimentological evidence (Pickford, 1981). Faunal list of the Maboko Fauna is as follows (Bishop, 1967).

Mammalia

Primates

*Proconsul nyanzae*

*Kenyapithecus africanus*

? *Mesopithecus* sp.

*Anasinopa leakeyi*

Hyracoidea

*Megalohyrax championi*

Proboscidea

*Gomphotherium* sp.

*Deinotherium* sp.

Perissodactyla

Rhinocerotidae

Artiodactyla

Suidae

Tragulidae

*Dorcatherium pigotti*

*Dorcatherium chappuisi*

*Dorcatherium parvum*

*Brachyodus aequatorialis*

#### (12) Aka Aitepuh (Kenya)

The age of this fauna was determined as 11.5-15 Ma by K-Ar dating and as Faunal Set III by faunal assemblages (Pickford & Kuga, in press). However, radiometric age indicate Faunal Set IV. Richness of Primates indicates woodland fauna. Faunal list of the Aka Aitepuh Fauna is shown in the previous chapter (p. 8-9).

#### (13) Fort Ternan (Kenya)

The age of this fauna was determined as 12.5-14 Ma by K-Ar dating and as Faunal Set IV by faunal assemblages (Pickford, 1981). Faunal list of the Fort Ternan Fauna is as follows (Bishop, 1967; Pickford, 1981).

Mammalia

## Primates

*Kenyapithecus wickeri*? *Proconsul nyanzae*

## Cercopithecidae

## Rodentia

*Kenyamys leakeyi*

## Carnivora

## Proboscidea

## Gomphotheriidae

## Artiodactyla

## Ruminants

## Suidae

## Giraffidae

## Hippopotamidae

*Kenyapotamus ternani*

## (14) Ngorora (Kenya)

The age of this fauna was determined as 10.2-12.7 Ma by K-Ar dating and stratigraphic position (Chapman & Brook, 1978; Pickford, 1978a; Hill et al., 1985). This fauna represents Faunal Set V of the East Africa (Pickford, 1981). Faunal list of the Ngorora A-D Formation is as follows (Benefit & Pickford, 1986).

## Mammalia

## Primates

Hominoidea large sp.

Hominoidea small sp.

Cercopithecoidea indet.

## Carnivora

*Agnotherium* sp.*Eomellivora* sp.*Sivaonyx* sp.*Percrocuta tobieni*

Canidae small sp.

## Tubulidentata

*Orycteropus chemeldoi*

## Proboscidea

*Choerolophodon ngorora**Tetralophodon* sp.*Deinotherium* sp. cf. *bozasi*

## Hyracoidea

*Parapliohyrax* sp.

## Perissodactyla

*Chilotheridium pattersoni**Aceratherium* or *Dicerorhinus**Brachypotherium* cf. *lewisi*

## Artiodactyla

? *Conohyus* sp.

*Lopholistriodon kidogosana*

Tayassuidae

*Kenyapotamus coryndoni*

Tragulidae

*Dorcatherium* cf. *pigotti*

*Palaeotragus primaevus*

? *Samotherium* sp.

*Climacoceras gentryi*

*Protragocerus labidotus*

*Sivoreas eremita*

*Homoidorcas tugenium*

? *Antidorcas* sp.

*Pseudotragus* ? *gentryi*

*Pachytragus* aff. *solignaci*

#### (15) Ngorora upper E (Kenya)

The age of this fauna was determined as Faunal Set VI by faunal assemblages. Faunal list of the Ngorora upper E Formation is as follows (Benefit & Pickford, 1986).

Mammalia

Proboscidea

*Choerolophodon ngorora*

Hyracoidea

*Parapliohyrax* sp.

Perissodactyla

*Hipparion primigenium*

Artiodactyla

*Kenyapotamus coryndoni*

*Palaeotragus primaevus*

*Pseudotragus* ? *gentryi*

#### (16) Ngeringerowa (Kenya)

The age of this fauna was determined as Faunal Set VI by faunal assemblages (Benefit & Pickford, 1986). Faunal list of the Ngeringerowa Fauna is as follows (Benefit & Pickford, 1986).

Mammalia

Primates

*Microcolobus tugenensis*

Proboscidea

*Deinotherium* sp. cf. *bozasi*

Perissodactyla

*Hipparion primigenium*

Artiodactyla

*Nyanzachoerus* sp.

*Kenyapotamus coryndoni*

*Palaeotragus primaevus*

? Hippotraginae or ? Reduncini

? *Antidorcas* sp.

(17) Nakali (Kenya)

The age of this fauna was determined as late Vallesian by correlation with Mediterranean mammalian fauna (Aguirre & Leakey, 1974; Aguirre & Guérin, 1974) and as Faunal Set VI by faunal assemblages (Benefit & Pickford, 1986). Nakali fauna is the nearest site of Namurungule fauna. Faunal list of the Nakali Formation is as follows (Benefit & Pickford, 1986).

Mammalia

Primates

Colobinae sp.

Proboscidea

? *Choerolophodon ngorora*

*Deinotherium* sp. cf. *bozasi*

Perissodactyla

*Hipparion primigenium*

*Kenyatherium bishopi*

Artiodactyla

*Nyanzachoerus* sp.

*Kenyapotamus* sp.

Tragulidae

*Dorcatherium* cf. *pigotti*

? *Palaeotragus primaevus*

? Hippotraginae or ? Reduncini

(18) Namurungule (Kenya)

The age of this fauna was determined as 7-10 Ma by K-Ar dating and stratigraphy and as the Turolian Fauna by faunal assemblages. Richness of equid and bovid taxa indicates openland fauna (Nakaya et al., 1984, in press). Faunal list of the Namurungule Formation is shown in the previous chapter (p. 9-11).

(19) Chorora (Middle Awash, Ethiopia)

The age of this fauna was determined as 9-10.5 Ma by radiometric dating. Faunal list of the Chorora Formation is as follows (Jacobs et al., 1980; Kalb et al., 1982a, 1982b, 1982c).

Mammalia

Rodentia

cf. *Dendromurinae*

*Paraulacodus johanesi*

*Paraphiomys* sp. 1

*Paraphiomys* sp. 2

Rodentia gen. et sp. indet.

Carnivora

*Homotherium* sp.

Proboscidea

Gomphotheriinae indet.



## Perissodactyla

*Hipparion* cf. *primigenium**Dicerorhinus* (*Stephanorhinus*) aff. *leakeyi*

## Artiodactyla

Suidae gen. et sp. indet.

? Palaeotraginae

Bovidae gen. et sp. indet.

## (20) Mpesida (Kenya)

The age of this fauna was determined as about 7 Ma. and as Faunal Set VII by faunal assemblages (Benefit & Pickford, 1986). Faunal list of the Mpesida Formation is as follows (Gentry, 1978a).

## Mammalia

## Artiodactyla

Tragelaphini

Antilopini

? Alcelaphini

Bovidae indet.

## (21) Lukeino (Kenya)

The age of the Member A of Lukeino Formation was determined as about 6.0-6.7 Ma and as Faunal Set VII by faunal assemblages (Benefit & Pickford, 1986). This fauna must have inhabited in lacustrine environments deduced from sedimentological evidence. Faunal list of the Member A and B of the Lukeino Formation is as follows (Pickford, 1978 b; Gentry, 1978a).

## Mammalia

## Primates

Cercopithecidae

Hominidae

## Lagomorpha

gen. et sp. indet.

## Rodentia

*Hystrix* sp.

gen. et sp. indet.

## Carnivora

*Enhydriodon*cf. *Ichneumia* sp.cf. *Crocuta*

Felidae gen. et sp. indet.

## Tubulidentata

*Orycteropus* sp.

## Proboscidea

*Anancus* sp.*Stegotetrabelodon* sp.*Primelephas* sp.*Deinotherium* sp.

*Hipparion* cf. *sitifense*  
 Chalicotheriidae  
 cf. *Ceratotherium* sp.  
*Nyanzachoerus tulotos*  
*Hippopotamus* sp.  
*Giraffa* sp.  
 Tragelaphini  
 Reduncini  
 Hippotragini  
 Neotragini  
 Antilopini cf. *Aepyceros*  
*Gazella* sp.  
 Cephalophini  
 Alcelaphini

## (22) Lothagam 1 (Kenya)

The age of this fauna was determined as before 3.7 Ma by K-Ar dating and stratigraphy and as Faunal Set VII by faunal assemblages (Benefit & Pickford, 1986). This fauna must have inhabited in fluvial environments deduced from sedimentological evidence (Behrensmeyer, 1976). Faunal list of the Lothagam 1 Formation is as follows (Smart, 1976).

### Mammalia

#### Primates

cf. *Parapapio* sp.  
 cf. *Cercocebus* sp.  
*Australopithecus* sp. cf. *africanus*

#### Rodentia

Anomaluridae (non gliding form)

#### Carnivora

*Civettictis* sp.  
*Euryboas* sp.  
 Felinae (large primitive form)  
 Machairodontinae

#### Tubulidentata

*Leptorycteropus guilielmi*

#### Proboscidea

Anancinae (primitive form)  
*Primelephas gomphotheroides*  
*Stegotetrabelodon orbus*  
*Deinotherium* sp.

#### Perissodactyla

*Hipparion primigenium*  
*Hipparion sitifense* (pygmy form)  
*Hipparion turkanense*  
*Brachypotherium lewisi*  
*Ceratotherium praecox*

## Artiodactyla

*Nyanzachoerus tulotos**Nyanzachoerus* aff. *jaegeri**Hippopotamus (Hexaprotodon)* sp. A*Hippopotamus (Hexaprotodon)* sp. B (pygmy form)*Giraffa* sp.*Pachytragus* aff. Hippotraginaeaff. *Kobus* sp.aff. *Redunca* sp.aff. *Aepyceros* sp.aff. *Damaliscus* sp.

Hippotragini

*Miotragocerus* sp.*Tragelaphus* sp. A*Tragelaphus* sp. B*Gazella* sp. A (large form)*Gazella* sp. B (small form)*Antilope* sp.Neotragini aff. *Rhynchotragus* sp.

## (23) Adu-Asa (Middle Awash, Ethiopia)

The age of this fauna was determined as the latest Miocene to earliest Pliocene by radiometric age and stratigraphy (Kalb et al., 1982a). Faunal list of the Adu-Asa Formation is as follows (Kalb et al., 1982a, 1982b, 1982c).

## Mammalia

Chiroptera indet.

Primates

cf. *Paracolobus chemeroni*

Colobinae indet. (Kuseralee type)

Rodentia gen. et sp. indet.

Carnivora

Felidae gen. et sp. indet.

Hyaenidae gen. et sp. indet.

Carnivora gen. et sp. indet.

Proboscidea

*Anancus* sp. A (cf. Lothagam type)*Anancus* sp. B (cf. *kenyensis*)*Stegotetabelodon* cf. *orbis*"Stegodibelodon" *schneideri**Primelephas* cf. *gomphotheroides*

aff. "Mammuthus subplanifrons"

*Deinotherium* sp. (small)

Perissodactyla

*Hipparion* cf. *primigenium**Hipparion* sp.*Diceros bicornis*

*Ceratotherium* cf. *praecox*

## Artiodactyla

*Nyanzachoerus kanamensis**Nyanzachoerus* cf. *tulotos**Kolpochoerus* sp. A*Hexaprotodon* sp. (large)*Sivatherium maurusium*

Giraffidae gen. et sp. indet.

*Miotragocerus* sp.*Kobus* cf. *subdolus**Tragelaphus* sp. (cf. Lothagam type)*Tragelaphus* aff. *nakuai*cf. *Gazella* sp.cf. *Ugandax gautieri*.cf. *Mesembriportax acrae*

Boselaphini indet.

Reduncini indet.

Hippotragini indet.

Alcelaphini indet.

Bovidae indet.

## (24) Sagantole (Middle Awash, Ethiopia)

The age of this fauna was determined as the early Pliocene by radiometric age and stratigraphy (Kalb et al., 1982a). Faunal list of the Sagantole Formation is as follows (Kalb et al., 1982a, 1982b, 1982c)

## Mammalia

## Primates

*Cercopithecus* sp.

cf. Papionini indet. (small)

*Parapapio* sp.*Theropithecus oswaldi* cf. *darti*

Rodentia gen. et sp. indet.

Carnivora indet.

## Proboscidea

*Anancus* sp. B (cf. *kenyensis*)*Anancus* sp. C (aff. *kenyensis*)*Anancus* sp. D (sp. nov.)*Mammuthus subplanifrons**Mammuthus* sp. nov. (Hadar type)*Elephas* cf. *ekorensis**Loxodonta adaurora**Deinotherium bozasi*

## Perissodactyla

*Hipparion* sp.

Rhinocerotidae gen. et sp. indet.

## Artiodactyla

*Nyanzachoerus kanamensis*  
*Nyanzachoerus jaegeri*  
*Kolpochoerus afarensis*  
*Notochoerus* cf. *eulius*  
*Hexaprotodon* sp. (large)  
*Sivatherium maurusium*  
*Miotragocerus* sp.  
*Kobus* cf. *subdolus*  
*Tragelaphus* aff. *nakuae*  
*Boselaphini* indet.  
*Hippotragini* indet.  
*Alcelaphini* indet.

*Bovidae* indet.

#### (25) Ekora (Kenya)

The age of this fauna was determined as 2.5-4 Ma by K-Ar dating. Faunal list of the Ekora Formation is as follows (Behrensmeyer, 1976).

Mammalia

Proboscidea

*Anancus* sp.  
*Elephas ekorensis*  
*Loxodonta adaurora*

Perissodactyla

*Ceratotherium praecox*

Artiodactyla

*Nyanzachoerus* cf. *plicatus*

#### (26) Kanapoi (Kenya)

The age of this fauna was determined as 2.5-4 Ma by K-Ar dating. This fauna must have inhabited in transitional (littoral, deltaic) environments deduced from sedimentological evidence. Faunal list of the Kanapoi Formation is as follows (Behrensmeyer, 1976).

Mammalia

Primates

*Parapapio jonesi*  
 cf. *Australopithecus*

Lagomorpha

*Lepus* sp.

Rodentia

*Hystrix* sp.  
*Tatera* sp.

Carnivora

*Enhydriodon* sp. nov.  
*Hyaena* sp.  
*Machairodontinae* indet.

Proboscidea

*Anancus* sp.

*Elephas ekorensis*

*Loxodonta adaurora*

*Deinotherium bozasi*

Perissodactyla

*Hipparion primigenium*

*Ceratotherium praecox*

Artiodactyla

*Nyanzachoerus pattersoni*

*Nyanzachoerus plicatus*

*Nyanzachoerus* spp.

*Notochoerus* cf. *capensis*

*Notochoerus* cf. *euilus*

*Hippopotamus* sp. nov.

*Giraffa* sp. nov.

*Giraffa* sp.

*Tragelaphus* sp.

*Reduncini* sp.

#### (27) Lothagam 3 (Kenya)

The age of this fauna was determined as after 3.7 Ma by K-Ar dating and stratigraphy and as Faunal Set VIII by faunal assemblages (Benefit & Pickford, 1986). This fauna must have inhabited in fluvial environments deduced from sedimentological evidence. Faunal list of the Lothagam 3 Formation is as follows (Behrensmeyer, 1976).

Mammalia

Primates

*Simopithecus* sp.

Proboscidea

*Loxodonta adaurora*

*Deinotherium bozasi*

Perissodactyla

*Hipparion (Stylohipparion)* sp.

Artiodactyla

*Nyanzachoerus plicatus*

*Notochoerus* cf. *euilus*

Hippopotamidae indet.

*Tragelaphus* sp.

Bovidae indet.

#### (28) Laetoli (Tanzania)

The age of this fauna was determined as 3.49-4.32 Ma by K-Ar dating (Drake & Curtis, 1987). In the upper Laetoli Beds, grass pollen predominates (50-80%) over that of the composite. This palynological evidence indicates short or medium grassland (Bonnefille et al., 1987). Faunal list of the Laetoli Bed is as follows (Leakey & Harris eds., 1987).

## Reptilia

## Testudinidae

*Geochelone (Aldabrachelys) laetoliensis**Geochelone (Geochelone) brachygularis*

## Serpentes

## Boidae

*Python sebae*

## Colubridae

cf. *Rhamphiophis* sp.

## Elapidae

*Naja robusta*

## Viperidae

*Bitis arietans* or *olduvaiensis*

## Aves

## Falconiformes

*Torgos* sp.

## Galiformes

*Francolinus* spp.*Numida* sp.

## Columbiformes

*Streptopelia* sp.

## Strigiformes

*Bubo* sp.

## Mammalia

## Macroscelidea

## Macroscelididae

*Rhynchocyon pliocaenicus*

## Insectivora

## Soricidae

? *Crocidura* sp.

## Primates

## Lorisidae

*Galago sadimanensis*

## Cercopithecidae

*Parapapio ado*cf. *Papio* sp.cf. *Paracolobus* sp.*Colobinae* gen. et sp. indet.

## Hominidae

*Australopithecus afarensis*

## Rodentia

## Sciuridae

*Paraxerus* sp.*Xerus* sp.*Xerus* cf. *janenschi*

## Cricetidae

*Gerbillinae* gen. et sp. indet.

*Tatera* cf. *inclusa*

*Dendromys* sp.

*Steatomys* sp.

*Saccostomus major*

Muridae

*Thallomys laetolilensis*

*Mastomys cinereus*

Muridae gen. et sp. indet.

Bathyergidae

*Heterocephalus quenstedti*

Hystriidae

*Hystrix leakeyi*

*Hystrix* cf. *makapanensis*

*Xenohystrix crassidens*

Lagomorpha

Pedetidae

*Pedetes laetoliensis*

*Pedetes* cf. *surdaster*

Leporidae

*Serengetilagus praecapensis*

Carnivora

Viverridae

*Herpestes (Galerella) palaeoserengensis*

*Herpestes (Herpestes) ichneumon*

*Helogale palaeogracilis*

? *Cynictis* sp.

*Mungos dietrichi*

*Viverra leakeyi*

Mustelidae

*Propoecilogale bolti*

*Mellivora capensis*

Canidae

? *Megacyon* sp.

aff. *Canis brevirostris*

*Vulpes* sp.

cf. *Otocyon* sp.

Canidae gen. et sp. indet.

Hyaenidae

*Crocota* sp. nov.

Hyaenidae spp.

Felidae

*Homotherium* sp.

*Dinofelis* sp.

*Leo* aff. *gombazogensis* or *palaeosinensis*

*Leo* cf. *pardus*

*Felis* spp.

Felidae gen. et sp. indet.



## Proboscidea

## Elephantidae

*Loxodonta exoptata*

## Deinotheriidae

*Deinotherium bozasi*

## Tubulidentata

## Orycteropodidae

*Orycteropus* sp.

## Perissodactyla

## Equidae

*Hipparion* cf. *ethiopicum**Hipparion* sp.

## Chalicotheriidae

*Ancylotherium hennigi*

## Rhinocerotidae

*Cetatotherium praecox**Diceros bocornis*

## Artiodactyla

## Suidae

*Notochoerus euilus**Potamochoerus porcus**Kolpochoerus limnetes*

## Giraffidae

*Giraffa stillei**Giraffa jumae**Giraffa* cf. *jumae**Sivatherium maurusium**Sivatherium* cf. *maurusium*

## Camelidae

*Camelus* sp.

## Bovidae

## Tragelaphini

*Tragelaphus* sp.

## Bovini

*Simatherium kohllarseni**Brabovus nanincisus*

## Hippotragini

*Praedamalis deturi*

? Hippotragini sp. nov.

## Alcelaphini

*Parmularius pandatus*

Alcelaphini sp. indet.

## Neotragini

*Madoqua avifluminis*? *Raphicerus* sp.

## Antilopini

*Gazella janenschi*

Tribe et gen. indet. aff. *Pelea* sp.

Bovidae indet.

(29) Langebaanweg (South Africa)

The age of the Verswater Formation in 'E' Quarry, Langebaanweg was determined as 4-6 Ma by faunal assemblage and stratigraphy. Marine to Littoral (Bed 1), Estuarine and Terrestrial (Bed 2) and Estuarine (Bed 3) environments were shown by sedimentological evidence. Marine invertebrates and shark teeth were yielded in the phosphate of the Bed 1. This fauna must have inhabited in Marine (Bed 1) and Estuarine (Bed 2 and 3) Faunal Units (Hendey, 1974). Faunal list of the Verswater Formation is as follows (Boné & Singer, 1965; Hendey, 1974; Gentry, 1980).

Mollusca

*Trigonephrus* sp.

Selachii

*Isurus* cf. *glaucus*

*Lamna nasus*

*Carcharias* sp.

*Carcharias ferox*

*Rhinoptera* cf. *dubia*

*Glopias vulpes*

Reptilia

cf. *Testudo* sp.

Aves

cf. *Struthio* sp.

Mammalia

Insectivora

*Elephantulus* sp.

Soricidae spp.

*Chrysochloris* sp.

Primates

cf. Cercopithecidae

Rodentia

Muridae spp.

Bathyergidae spp.

Lagomorpha

gen. et sp. indet.

Pholidota

cf. *Manis* sp.

Tubulidentata

*Orycteropus* sp.

Carnivora

Phocidae

*Prionodelphis capensis*

Ursidae

*Agriotherium africanum*

Viverridae

*Herpestes* spp.

*Viverra leakeyi*

*Genetta* sp.

Mustelidae

*Mellivora* aff. *punjabiensis*

*Enhydriodon africanus*

Canidae

Canidae gen. et sp. indet.

Hyaenidae

*Percrocuta australis*

*Hyaena abronia*

*Hyaena* sp. B

*Hyaenictis preforfex*

Hyaenidae gen. et sp. indet.

Felidae

*Machairodus* sp.

cf. *Homotherium* sp.

*Dinofelis diastemata*

*Felis* aff. *issiodorensis*

*Felis obscura*

Cetacea

fam. gen. et sp. indet.

Hyracoidea

cf. *Procavia antiqua*

Proboscidea

Gomphotheriidae

Elephantidae

*Mammuthus subplanifrons*

Perissodactyla

Equidae

*Hipparion albertense baardi*

Rhinocerotidae

*Cetatotherium praecox*

Artiodactyla

Suidae

*Nyanzachoerus* sp.

aff. *Diamantohyus*

*Libytherium oldvaiense*

Giraffidae

*Giraffa gracilis*

Bovidae

Tragelaphini

*Tragelaphus* spp.

Bovini

*Simatherium demissum*

Boselaphini

*Mesembriportax acrae*

## Reduncini

*Kobus subdolus**Kobus* spp.

## Alcelaphini

*Damalacra neanica**Damalacra acalla*

## Neotragini

*Raphicerus partalius*

## Antilopini

*Gazella* sp.

## Ovibovini gen. et sp. indet.

Large Mammal Faunal Range Chart of Neogene East Africa is compiled mainly from Pickford (1981), Pickford et al. (1984), Benefit & Pickford (1986), Nakaya (1987, 1989, 1993) and Nakaya et al. (1984, in press) in the next chapter (Table 7). Many taxa of Neogene Sub-Saharan Africa are represented by incomplete fossil remains. Identification of some species from East Africa are problematic. Therefore, in the next chapter, I use specific names for complete or distinguished remains and generic, genus group, and tribal names for incomplete materials from the Neogene Sub-Saharan Africa.

## DISCUSSION

## I. Statistical Analysis of Faunal Resemblance between Sub-Saharan Africa and Eurasia

The faunal resemblance of mammalian faunas of Sub-Saharan Africa and Eurasia is analyzed in this chapter.

Mammal provinces of Miocene Africa and Eurasia were divided into five areas (Africa, Iberian, Europe, West Asia and India) by Coryndon & Savage (1973) and Bernor (1983, 1984) proposed eight provinces (Southwest Europe, East and Central Europe, Roumania-West C.I.S., Sub-Paratethys, North Africa, Siwalik, East Africa and China). In this work, mammalian provinces are followed largely the scheme of Bernor (1983, 1984). East African province (Bernor, 1983, 1984) is the same as Sub-Saharan, and Roumania-West C.I.S. (Bernor, 1983, 1984) province is included in Sub-Paratethys in this work.

Previous researchers emphasized the Miocene faunal connection between Sub-Saharan Africa and Siwaliks (general: Coryndon & Savage, 1973; Bovidae: Thomas, 1979, 1981; Hipparionine: Bernor & Hussain, 1985). However, it has been pointed out that the discussion of connection between Sub-Saharan Africa and Siwaliks is based largely on fragmental remains from the middle to late Miocene Sub-Saharan sites. The following discussion of the biogeography between Sub-Saharan and Eurasia is based on new and rich mammalian fossils from the late Miocene Namurungule Formation, Samburu Hills, Northern Kenya.

Statistical approaches are very useful for analyzing the resemblance of faunas. Simpson's formula is simple and useful for analyzing resemblance between two faunal

assemblages. This index is dividing the common taxa numbers by the total taxa numbers of smaller fauna. Cluster analysis is also useful for multivariate analysis between faunas of Sub-Saharan Africa and Eurasia. In this thesis, the author analyzed species, genera and families of Sub-Saharan Africa and Eurasian faunas by Simpson's Index and genera and families of the same area by cluster analysis. Because subfamily and tribe are not mainly used in classification except Rhinocerotidae (Perissodactyla) and Bovidae (Artiodactyla) in both statistic methods and common taxa are very few in the specific level for using cluster analysis.

Over 500 taxa from the following mammalian fauna are analyzed by Simpson's Index (Simpson, 1960) and cluster analysis (Tanaka et al. eds., 1984).

Namurungule (early Turolian, Samburu Hills, Kenya), Aka Aiteputh (Astaracian, Samburu Hills, Kenya), Kongia (late Turolian, Samburu Hills, Kenya), Ngorora (Vallesian, Baringo Basin, Kenya), Ngorora upper E (early Turolian, Baringo Basin, Kenya), Ngeringerowa (early Turolian, Baringo Basin, Kenya), Nakali (early Turolian, Baringo Basin, Kenya), Mpesida (late Turolian, north Baringo Basin, Kenya), Lukeino (late Turolian, north Baringo Basin, Kenya), Bou Hanifia (late Vallesian, Algeria), Sahabi (Turolian, Libya), Eppelsheim (late Vallesian, West Germany), Dorn-Dürkheim (late Turolian, West Germany), Mt. Lebéron (early Turolian, France), Pikermi (middle Turolian, Greece), Maragheh (Turolian, Iran), Samos (early to middle Turolian Greece), Chinji (Astaracian, Pakistan), Nagri (late Vallesian or early Turolian, Pakistan), Dhok Pathan (late Turolian, Pakistan), Baode (early Turolian, Shanxi, China), Yushe Zone I (late Turolian, Shanxi, China) (Table 2).

Faunal resemblance is analyzed by various statistic methods. Faunal resemblance of two faunas is calculated by the following formulas (Shuey et al., 1978).

1. Jaccard

$$\frac{C}{N_A + N_B - C}$$

2. Burt-Pilot

$$\frac{2C}{N_A + N_B}$$

3. Kulczynski

$$\frac{C(N_A + N_B)}{2N_A N_B}$$

4. Otsuka

$$\frac{C}{\sqrt{N_A N_B}}$$

5. Simpson

$$\frac{C}{N_1}$$

6. Braun-Blaunquet

$$\frac{C}{N_2}$$

C is common taxa number of two faunas,  $N_A$  is total taxa number of A Fauna,  $N_B$  is

total taxa number of B Fauna, N1 is total taxa number of smaller fauna, N2 is total taxa number of larger fauna.

Simpson's formula is the simplest and has little influence of sample size and emphasizes faunal resemblance (Simpson, 1960). Simpson's Index is shown on percentage:

$$\frac{C \times 100}{N_1}$$

The author examined faunal resemblance of each two faunas by Simpson's index. In the specific level, the Namurungule Fauna indicates the resemblance to the following East and North African faunas; Nakali (50%), Ngorora upper E (33.33%), Ngeringerowa (33.3%), Lukeino (33.3%), and Bou Hanifia (33.33%) (Table 4). In the generic level, the Namurungule Fauna indicates the resemblance to the following faunas of East and North Africa and Sub-Paratethys; Nakali (75%), Ngorora upper E (57.14%), Ngeringerowa (55.56%), Bou Hanifia (50%) and Samos (44.44%), Mpesida (40%) (Table 5). In the family level, the Namurungule Fauna indicates the resemblance to the following faunas of East and North Africa and Southwestern and Central Europe; Bou Hanifia (100%), Ngorora upper E (85.71%), Mt. Lebéron (83.33%), Eppelsheim (83.33%) and Mpesida (80%) (Table 6).

The reciprocal number of Simpson's index ( $N_1/C$ ) is used for showing the dissimilarity on the group average method of cluster analysis (by CLUST program, Tanaka et al., 1984). In the case that Simpson's index is zero, the dissimilarity is uncountable. Therefore, analysis of all faunas in the case of species and the Aka Aiteputh and Dorn-Dürkheim faunas in the case of genera are omitted from the cluster analysis. In the generic level, the Namurungule and only East African faunas make large cluster (Nakali; firstly, Ngorora upper E; secondly, Ngorora and Ngeringerowa; thirdly) (Fig. 10). The Namurungule, East and North African and west European faunas make large cluster (Bou Hanifia; firstly, Nakali, Mt. Lebéron and Sahabi; secondly) in family level (Fig. 11). Using the raw data of Sub-Saharan and Eurasian faunas, faunal resemblance of each fauna was examined by group average method in cluster analysis on the basis of dissimilarity of Minkowsky distance (by CLUST program, Tanaka et al. eds., 1984). In the generic level, the Namurungule and East (Aka Aiteputh, Kongia, Ngorora E, Ngeringerowa, Nakali, and Lukeino) and North African (Bou Hanifia) and South-Western European (Mt. Lebéron) faunas make first large cluster and Dorn-Dürkheim faunas make next large cluster (Fig. 12). In the family level, the Namurungule and Eppelsheim faunas make first cluster, Lukeino faunas make next cluster, and Kongia, Mpesida, Bou Hanifia, Mt. Lebéron, Ngorora E, Ngeringerowa, Nakali and Dhok Pathan faunas make next large cluster (Fig. 13).

The Namurungule Fauna resembles faunas of Astaracian to late Turolian East Africa firstly, late Vallesian to Turolian North African faunas secondly, late Vallesian to Turolian Central and Southwest European faunas thirdly, early to middle Turolian Sub-Paratethys fauna and late Turolian Siwalik fauna lastly. On the basis of the above results, the Namurungule Fauna indicates similarity with the faunas of North Africa, South Western Europe and Sub-Paratethys.

**Table 4.** Faunal resemblance of the Namurungule Fauna, African and Eurasian faunas in specific level by the Simpson's index.

	NM	AA	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
NM	NM(9)		1	2	2	2	1		2	1											
AA	0	AA(10)	2		1																
NG	11.11	20	NG(15)	4	4	2		1								1					
NE	33.33	0	66.67	NE(6)	4	4			1	1											
NW	33.33	16.67	66.67	66.67	NW(6)	3			1	1						1					
NK	50	0	50	100	75	NK(4)			1	1											
LK	33.33	0	0	0	0	0	LK(3)	1	1												
MP	0	0	50	0	0	0	50	MP(2)		1											
SB	22.22	0	0	16.67	16.67	25	33.33	0	SB(25)		1		2	2	2						1
BH	33.33	0	0	33.33	33.33	33.33	0	50	0	BH(3)											
ML	0	0	0	0	0	0	0	0	12.5	0	ML(8)		3	3	2						1
EP	0	0	0	0	0	0	0	0	0	0	0	EP(22)	3	3							2
PK	0	0	0	0	0	0	0	0	8	0	37.5	13.64	PK(64)	42	19						3
SM	0	0	0	0	0	0	0	0	8	0	37.5	13.64	65.63	SM(82)	26				2	1	2
MG	0	0	0	0	0	0	0	0	8	0	25	0	48.72	66.67	MG(39)				1		1
CJ	0	0	6.667	0	16.67	0	0	0	0	0	0	0	0	0	0	CJ(44)					
NR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	NR(59)				
DP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	DP(22)			
BD	0	0	0	0	0	0	0	0	0	0	0	0	0	3.333	2.564	0	0	0	BD(60)	14	
YS	0	0	0	0	0	0	0	0	0	0	0	0	0	2.222	0	0	0	0	31.11	YS(45)	
DD	0	0	0	0	0	0	0	0	4.762	0	12.5	9.524	14.29	9.524	4.762	0	0	0	0	0	DD(21)

Note: NM; Namurungule, AA; Aka Aiteputh, KG; Kongia, NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa, NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Lebéron, EP; Eppelsheim, PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe, DD; Dorn-Dürkheim. Total number of taxa is put in parentheses.

**Table 5.** Faunal resemblance of the Namurungule Fauna, African and Eurasian faunas in generic level by the Simpson's index.

	NM	AA	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
NM	NM(18)	1	6	4	5	6	4	2	5	2	2	4	7	8	7	3	4	2	6	5	3
AA	8.333	AA(12)	3		1							1		1		1	1				
NG	33.33	25	NG(28)	5	7	3	1	2	2	1	3	5	7	10	6	9	9	3	5	6	1
NE	57.14	0	71.43	NE(7)	4	5	2	1	1	1	1	2	4	5	3	2	3	1	2	2	1
NW	55.56	11.11	77.78	57.14	NW(9)	5	3	1	2	2	2	3	6	7	4	3	3	2	2	3	1
NK	75	0	37.5	71.43	62.5	NK(8)	3	1	2	2	2	2	5	5	4	1	3	2	2	2	1
LK	26.67	0	6.667	28.57	33.33	37.5	LK(15)	3	4	1	1	2	5	6	3	3	4	3	2	3	1
MP	40	0	40	20	20	20	60	MP(5)	3	1	1	2	2	2	1	2	2	2	1	1	
SB	27.78	0	7.143	14.29	22.22	25	26.67	60	SB(34)	2	5	3	10	10	10	5	5	3	3	1	2
BH	50	0	25	25	50	50	25	25	50	BH(4)	3	2	3	3	2	2	2	1	3	2	
ML	20	0	30	14.29	22.22	25	10	20	50	75	ML(10)	5	6	5	4	4	3	2	2	2	2
EP	22.22	8.333	27.78	28.57	33.33	25	13.33	40	16.67	50	50	EP(18)	7	5	2	9	9	5	3	4	3
PK	38.89	0	25	57.14	66.67	62.5	33.33	40	29.41	75	60	38.89	PK(56)	37	22	10	9	5	11	11	6
SM	44.44	8.333	35.71	71.43	77.78	62.5	40	40	29.41	75	50	27.78	66.07	SM(58)	26	10	13	7	14	10	6
MG	38.89	0	21.43	42.86	44.44	50	20	20	29.41	50	40	11.11	64.71	76.47	MG(34)	6	6	3	11	7	3
CJ	16.67	8.333	32.14	28.57	33.33	12.5	20	40	14.71	50	40	50	20	20	17.65	CJ(50)	30	12	5	4	
NR	22.22	8.333	32.14	42.86	33.33	37.5	26.67	40	14.71	50	30	50	16.07	22.41	17.65	60	NR(62)	19	7	7	2
DP	11.11	8.333	14.29	14.29	22.22	25	20	40	14.29	25	20	27.78	23.81	33.33	14.29	57.14	90.48	DP(21)	5	4	
BD	33.33	0	17.86	28.57	22.22	25	13.33	20	8.824	75	20	16.67	31.43	40	32.35	14.29	20	23.81	BD(35)	18	3
YS	27.78	0	21.43	28.57	33.33	25	20	20	2.941	50	20	22.22	32.35	29.41	20.59	11.76	20.59	19.05	52.94	YS(34)	2
DD	16.67	0	3.704	14.29	11.11	12.5	6.667	0	7.407	0	20	16.67	22.22	22.22	11.11	0	7.407	0	11.11	7.407	DD(27)

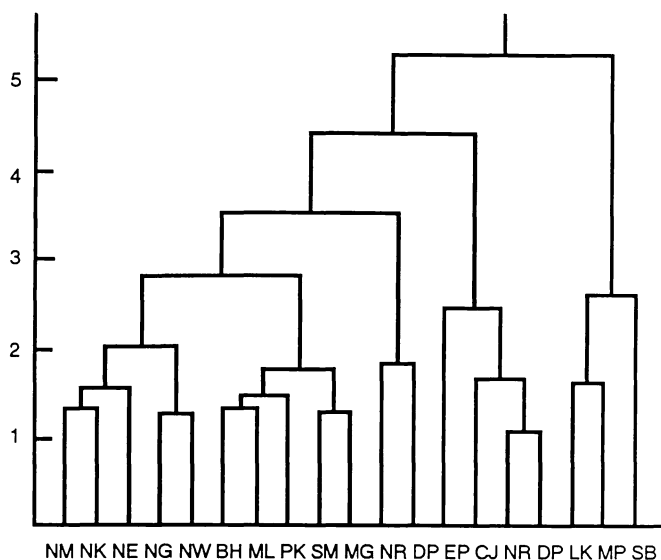
Note: NM; Namurungule, AA; Aka Aiteputh, KG; Kongia, NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa, NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Lebéron, EP; Eppelsheim, PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe, DD; Dorn-Dürkheim. Total number of taxa is put in parentheses.



**Table 6.** Faunal resemblance of the Namurungule Fauna, African and Eurasian faunas in family level by the Simpson's index.

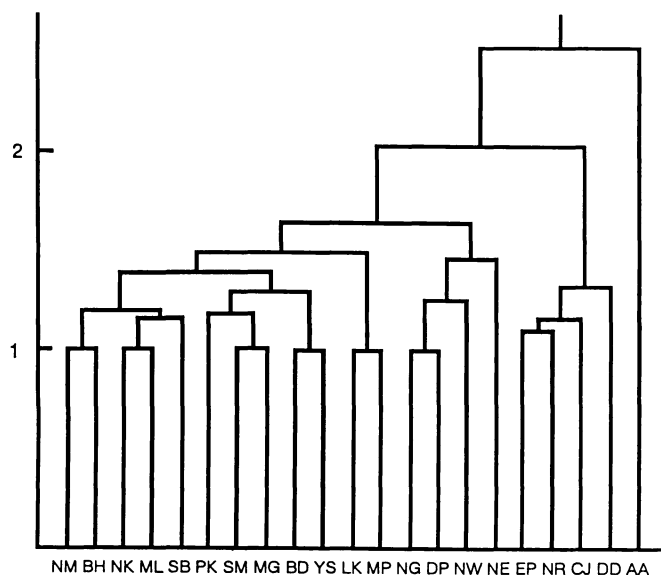
NM	AA	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
NM(15)	7	10	6	6	10	11	4	11	5	5	10	10	10	9	10	10	7	8	8	3
AA 58.33	AA(12)	10	4	4	6	5	1	5	2	2	6	6	7	4	6	7	5	4	4	2
NG 66.67	83.33	NG(18)	6	7	11	12	3	10	4	4	8	11	12	10	10	12	12	12	13	4
NE 85.71	57.14	85.71	NE(7)	5	6	5	3	5	2	1	3	6	6	4	4	4	4	4	4	2
NW 75	50	87.5	71.43	NW(8)	7	6	3	6	3	2	4	6	6	5	5	5	6	4	4	1
NK 76.92	50	84.62	85.71	87.5	NK(13)	10	4	10	5	6	7	10	9	9	9	9	8	8	8	3
LK 73.33	41.67	66.67	71.43	75	76.92	LK(18)	5	12	5	6	9	11	11	10	12	13	9	7	7	4
MP 80	20	60	60	60	80	100	MP(5)	5	3	2	2	5	5	3	4	3	4	3	3	
SB 73.33	41.67	55.56	71.43	75	76.92	66.67	100	SB(24)	5	6	8	13	13	11	12	12	8	9	10	6
BH 100	40	80	40	60	100	100	60	100	BH(5)	4	5	5	5	5	5	5	5	5	5	1
ML 83.33	33.33	66.67	16.67	33.33	100	100	40	100	80	ML(6)	5	5	5	5	6	6	4	5	5	2
EP 83.33	50	66.67	42.86	50	58.33	75	40	66.67	80	83.33	EP(12)	10	10	8	10	11	7	7	7	8
PK 66.67	50	61.11	85.71	75	76.92	61.11	100	54.17	100	83.33	83.33	PK(25)	19	14	13	13	9	7	13	8
SM 66.67	58.33	66.67	85.71	75	69.23	61.11	100	54.17	100	83.33	83.33	79.17	SM(24)	15	15	13	9	11	12	8
MG 60	33.33	66.67	57.14	62.5	69.23	66.67	60	73.33	100	83.33	66.67	93.33	100	MG(15)	10	11	7	11	11	5
CJ 66.67	50	55.56	57.14	62.5	69.23	66.67	80	60	100	100	83.33	65	75	66.67	CJ(20)	18	11	8	8	7
NR 66.67	58.33	66.67	57.14	62.5	69.23	72.22	60	50	100	100	91.67	52	54.17	73.33	90	NR(25)	10	8	8	8
DP 58.33	41.67	100	57.14	75	66.67	75	80	66.67	100	66.67	58.33	75	75	58.33	91.67	83.33	DP(12)	6	6	3
BD 66.67	33.33	100	57.14	50	66.67	58.33	60	75	100	83.33	58.33	58.33	91.67	91.67	66.67	66.67	50	BD(12)	12	5
YS 53.33	33.33	86.67	57.14	50	61.54	46.67	60	66.67	100	83.33	58.33	86.67	80	73.33	53.33	53.33	50	100	YS(15)	6
DD 30	20	40	28.57	12.5	30	40	0	60	20	33.33	80	80	80	50	70	80	30	50	60	DD(10)

Note: NM; Namurungule, AA; Aka Aiteputh, KG; Kongia, NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa, NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Lebérón, EP; Eppelsheim, PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe, DD; Dorn-Dürkheim. Total number of taxa is put in parentheses.

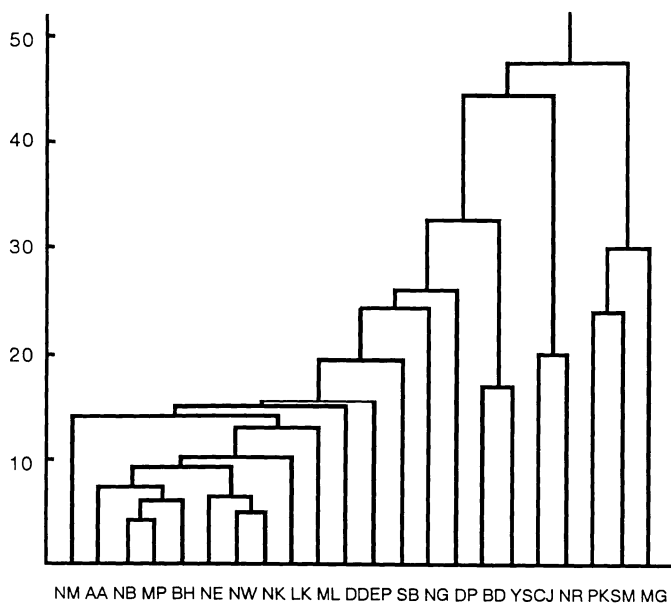


**Fig. 10.** Dendrogram by the cluster analysis on the basis of the faunal dissimilarity of the Namurungule Fauna, African and Eurasian faunas (in generic level by the reciprocal number of Simpson's index).

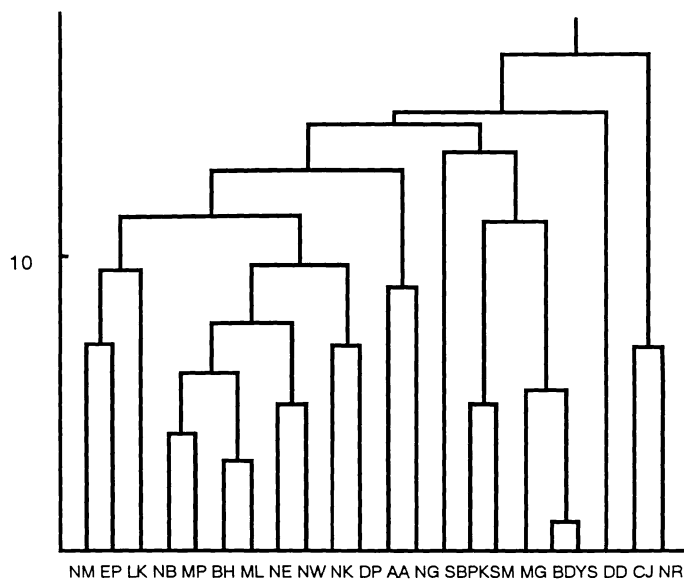
AA: Aka Aiteputh; BD: Baode; BH: Bou Hanifia; CJ: Chinji; DD: Dorn- Dürkheim; DP: Dhok Pathan; EP: Eppelsheim; NB: Kongia; LK: Lukeino; MG: Maragheh; ML: Mt. Lebéron; MP: Mpesida; NE: Ngorora upper E; NG: Ngorora; NK: Nakali; NM: Namurungule; NW: Ngeringerowa; PK: Pikermi; SB: Sahabi; SM: Samos; YS: Yushe.



**Fig. 11.** Dendrogram by the cluster analysis on the basis of the faunal dissimilarity of the Namurungule Fauna, African and Eurasian faunas (in family level by the reciprocal number of Simpson's index).



**Fig. 12.** Dendrogram by the cluster analysis on the basis of taxa of the typical Astaracian to Turolian African and Eurasian faunas (in generic level by Minkowsky's distance).



**Fig. 13.** Dendrogram by the cluster analysis on the basis of taxa of the typical Astaracian to Turolian African and Eurasian faunas (in family level by Minkowsky's distance).

**Table 7.** Range chart of mammalian faunas from the Neogene Sub-Saharan Africa.

Taxa	Order / Age	22	20	18	16.5	15	12.5	10.5	7.5	5.5	(Ma)
<i>Paraphiomys pigotti</i>	Rodentia	-----									
<i>Walangania africanus</i>	Artiodactyla	-----									
<i>Creodonta</i>	Creodonta	-----									
<i>Archaeobelodon aff. filholi</i>	Proboscidea	-----									
<i>Prodeinotherium hopleyi</i>	Proboscidea	-----									
<i>Proconsul</i> ?	Primates	-----									
<i>Aceratherium/Dicerorhinus</i>	Perissodactyla	-----									
<i>Megalohyrax championi</i>	Hyracoidea	-----									
<i>Diamantohyus africanus</i>	Artiodactyla	-----									
<i>Libycochoerus</i>	Artiodactyla	-----									
<i>Dorcatherium chappuisi</i>	Artiodactyla	-----									
<i>Dorcatherium pigotti</i>	Artiodactyla	-----									
<i>Chalicotherium</i>	Perissodactyla	-----									
<i>Hemimeryx</i>	Artiodactyla	-----									
<i>Chilotheridium</i>	Perissodactyla	-----									
<i>Kenyaipithecus</i>	Primates	-----									
<i>Palaeotragus</i>	Artiodactyla	-----									
<i>Gazella</i>	Artiodactyla	-----									
<i>Rangwapithecus</i>	Primates	-----									
<i>Oreopithecidae</i> nov. gen.	Primates	-----									
<i>Lopholistrion</i>	Artiodactyla	-----									
<i>Climacoceras gentryi</i>	Artiodactyla	-----									
<i>Kenyaipotamus temani</i>	Artiodactyla	-----									
Hominoidea small form	Primates	-----									
<i>Conohyus</i> ?	Artiodactyla	-----									
Tayassuidae	Artiodactyla	-----									
<i>Choerolophodon</i>	Proboscidea	-----									
<i>Paradiceros</i>	Perissodactyla	-----									
<i>Kenyaipotamus coryndonii</i>	Artiodactyla	-----									
<i>Oiocerus</i>	Artiodactyla	-----									
<i>Listriodon</i>	Artiodactyla	-----									
<i>Protragocerus</i>	Artiodactyla	-----									
<i>Caprotragoides gentryi</i>	Artiodactyla	-----									
<i>Agnotherium</i>	Carnivora	-----									
<i>Orycteropus chemoi</i>	Tubulidentata	-----									
Hyaenidae (Percrocuta)	Carnivora	-----									
Giraffidae large form (Samotherium)	Artiodactyla	-----									
<i>Paraplioherax</i>	Hyracoidea	-----									
<i>Homoiodorcas</i>	Artiodactyla	-----									
<i>Pachytragus</i>	Artiodactyla	-----									
<i>Sivoreas/Palaeoreas</i>	Artiodactyla	-----									
<i>Tetralophodon</i>	Proboscidea	-----									
<i>Brachypotherium lewisi</i>	Perissodactyla	-----									
<i>Deinotherium</i>	Proboscidea	-----									
Small Colobines	Primates	-----									
<i>Paraulacodus</i>	Rodentia	-----									
Hominoidea large form	Primates	-----									
<i>Kenyaitherium bishopi</i>	Perissodactyla	-----									
Hipparion large form	Perissodactyla	-----									
<i>Nyanzachoerus</i>	Artiodactyla	-----									
Hippotraginae/Reduncini	Artiodactyla	-----									
<i>Ancylotherium</i>	Perissodactyla	-----									
Hipparion small form	Perissodactyla	-----									
<i>Ceratotherium</i>	Perissodactyla	-----									
<i>Hippopotamus</i>	Artiodactyla	-----									
<i>Stegotetrabelodon</i>	Proboscidea	-----									
<i>Primelephas</i>	Proboscidea	-----									
<i>Anancus</i>	Proboscidea	-----									
<i>Tragelaphus</i>	Artiodactyla	-----									
<i>Giraffa</i>	Artiodactyla	-----									
<i>Crocota</i> ?	Carnivora	-----									
<i>Madoqua</i>	Artiodactyla	-----									
<i>Kobus</i>	Artiodactyla	-----									
<i>Enhydriodon</i>	Carnivora	-----									
<i>Ugandax</i>	Artiodactyla	-----									
<i>Cephalophus</i>	Artiodactyla	-----									
<i>Aepycerus</i>	Artiodactyla	-----									

Faunal Sets Pre Set I I II III IV V VI VII VIII

Source: Pickford, 1981; Pickford et al., 1984; Benefit &amp; Pickford, 1986; Nakaya, 1987, 1989, 1993; Nakaya et al., in press.

## II. Faunal Change of the Late Miocene Sub-Saharan Africa

In this chapter, the author analyzes faunal change of the Neogene mammalian faunas in Sub-Saharan Africa and establishes the position of the faunal turnover in Neogene Sub-Saharan Africa to the Namurungule Fauna.

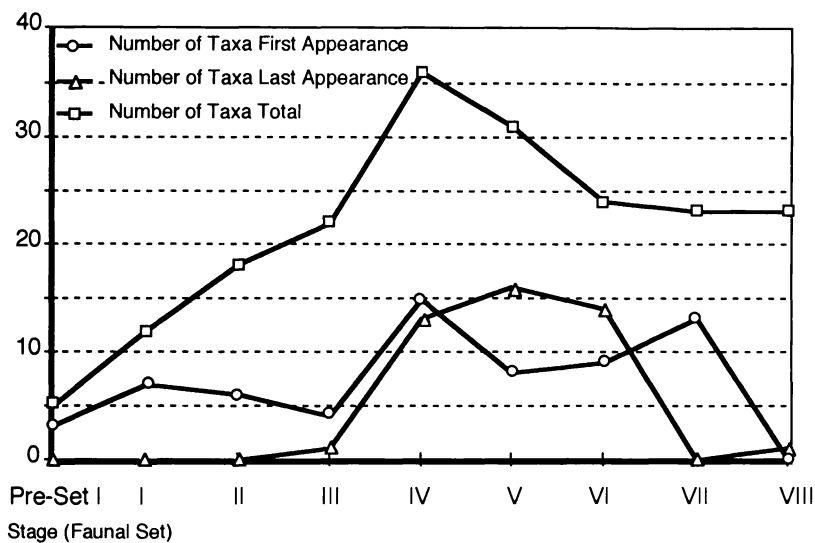
In faunal change of late Miocene East Africa, Maglio (1978) reviewed patterns of faunal evolution of Africa. According to Maglio (1978), the rate of endemism is constant through the Cenozoic Era, the rate of turn over has two peaks (from Eocene to early Miocene and Pliocene) in the Cenozoic Era and the rate of extinction decreased constantly by genera through Neogene in the Africa. Savage & Russell (1983) also studied faunal turnover in Europe and North America during Cenozoic Era. They examined the number of total, standing, first appearing, disappearing and running mean on the genera and family.

In this work, the first and last appearances of mammalian taxa from the Neogene Sub-Saharan Africa are considered in detail. The "Half-life" of fauna is analyzed in each order of mammals and each faunal set (mammalian stage in Sub-Saharan Africa). Furthermore, the faunal turnover of Sub-Saharan mammal through late Miocene is discussed.

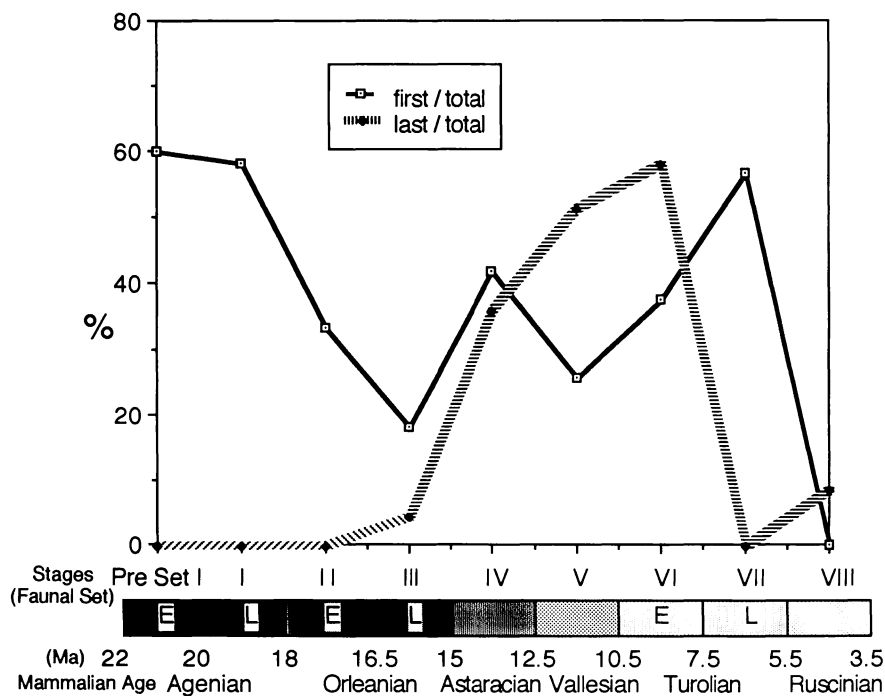
Table 7 shows range of the first appearance and last appearance of mammalian taxa (mainly species and genera of large mammals) from Neogene Sub-Saharan Africa.

Figure 14 is the numbers of the first, last appearance and total taxa in each faunal set. The number of the first appearance line has two peaks. The first peak (Set IV) indicates the appearance of the new Astaracian taxa. The second peak (Set VII) shows the appearance of the Pliocene taxa. The intermediate zone between two peaks (Set V and VI) also shows the appearance of the new late Miocene taxa. The number of the last appearance line has one broad peak. This peak (Set IV to VI) indicates constant extinction from the Astaracian to Turolian. The first and second peak of first appearance is comparable to the broad peak of the last appearance. The number of total taxa has one peak (Set IV). This peak shows rich faunal assemblage of the intermediate zone of old and new faunas in Miocene.

Figure 15 is the percentage of the first and last appearance of taxa by total taxa of each faunal set. The percentage of the first appearance has three peaks; the first peak (Pre Set I and Set I) indicates the first diversity of the Neogene fauna in the Sub-Saharan Africa, the second peak (Set IV) shows the diversity of middle Miocene fauna after the extinction of early Miocene taxa and the third peak (Set VII) indicates the diversity of late Miocene fauna after the extinction of middle Miocene taxa. The percentage of the last appearance shows one broad peak. The beginning of the peak (Set IV) indicates the extinction of many early Miocene taxa, the middle of the peak (Set V) shows the extinction of many early to middle Miocene taxa. The maximum of the peak indicates the extinction of almost all middle Miocene and some early late Miocene taxa. The second and third peak of first appearance is comparable to the broad peak of the last appearance. There is large gap of faunal turn over between Faunal Set III and IV. It is evident that this gap indicates some paleoenvironmental change.



**Fig. 14.** Number of the total, first appearance and last appearance mammalian taxa of each Faunal Set from the Neogene Sub-Saharan Africa.



**Fig. 15.** Percentage of the first appearance and last appearance mammalian taxa by total taxa of each Faunal Set from the Neogene Sub-Saharan Africa.

**Table 8.** Half-life of the total taxa of the mammalian faunas from the Neogene Sub-Saharan Africa.

Stage	FA0	I	II	III	IV	V	VI	VII	VIII
LA VIII	0	0	1	0	0	3	6	13	0
VII	0	0	0	0	0	0	0	0	0
VI	0	1	2	0	5	3	3		
V	1	2	0	3	8	2			
IV	4	4	3	0	2				
III	0	0	0	1					
II	0	0	0						
I	0	0							
Pre-Set I	0								
Number	67								
Cumulate	FA0	I	II	III	IV	V	VI	VII	VIII
LA VIII	0	0	1	1	1	4	10	23	23
VII	0	0	1	1	1	4	10	23	
VI	0	1	4	4	9	15	24		
V	1	4	7	10	23	31			
IV	5	12	18	21	36				
III	5	12	18	22					
II	5	12	18						
I	5	12							
Pre-Set I	5								

Stage	Previous	Next	Average	Half-life	HL Av.	Mean Long.
1stage	67.196	74.269	70.556	1.987	1.987	5.744
2stage	38.418	45.946	41.846	1.591	1.789	5.171
3stage	20.755	26.613	23.322	1.428	1.669	4.824
4stage	10.949	16.129	13.043	1.361	1.592	4.601
5stage	3.960	7.018	5.063	1.162	1.506	4.352
6stage	1.429	2.857	1.905	1.050	1.430	4.133
7stage	0.000	0.000	0.000			
8stage	0.000	0.000	0.000			

Result of "Half-life" analysis to total taxa.

Total time range	17 Ma	Half-life(Av.)	1.430 Stages
Number of faunal set	9 Stages	Mean Long.	4.133 Stages
Average of fauna range	1.889 Ma	Longevity	2.909 Stages
Half-life of fauna	2.701 Ma	Long. (all)	2.552 Stages
Range of fauna	7.806 Ma		

Note; Left upper table shows number of first and last appearance of total taxa.

Left lower table shows cumulate number of first and last appearance of total taxa.

Right upper table shows the result of calculation of "Half-life" in previous and

next stage and average of each stages. HL; half-life, FA; first appearance,

LA; last appearance, Long.; longevity, Av.; average.

In the next faunal analysis, the author examines half-life of fauna in Neogene Sub-Saharan Africa. Late Professor Björn Kurtén of University of Helsinki proposed “Half-life” concept (Kurtén, 1959, 1972, 1988). Following Kurtén, the half-life is based on the distribution by first and last appearances of taxa during unit stage, and is calculated by the cumulative distribution showing the total number of taxa, belonging to different temporal strata, present at a given time. The average percentage of previous-stages and next-stage taxa in a given fauna is obtained. The results happen to be identical in this case, but this is not always the case. A weighted mean percentage is obtained. The half-life, expressed with the local age as a unit is calculated. Weighted mean percentages for temporal strata in faunas two stages apart are obtained in analogous way. The half-life is calculated on this basis. In this case, three-stages survival could be used to check the estimates based on one and two-stage survival, and the author repeated the same calculation until stage that reveals no survival. The half-life of fauna is different on the basis of taxa, space and time. The author calculate the half-life and mean longevity of fauna based on taxa and faunal sets.

In the case of half-life of fauna based on taxa, half-life of total taxa is 1.43 (Faunal set) stage (2.70 Ma) (Table 8), Proboscidea is 1.99 stage (3.75 Ma), Perissodactyla is 1.79 stage (3.38 Ma), Carnivora (including Creodonta) is 1.52 stage (2.87 Ma), Artiodactyla is 1.48 stage (2.79 Ma), Primates is 1.30 stage (2.46 Ma), Hyracoidea is 1.52 stage (2.88 Ma), Rodentia is 2.53 stage (4.77 Ma).

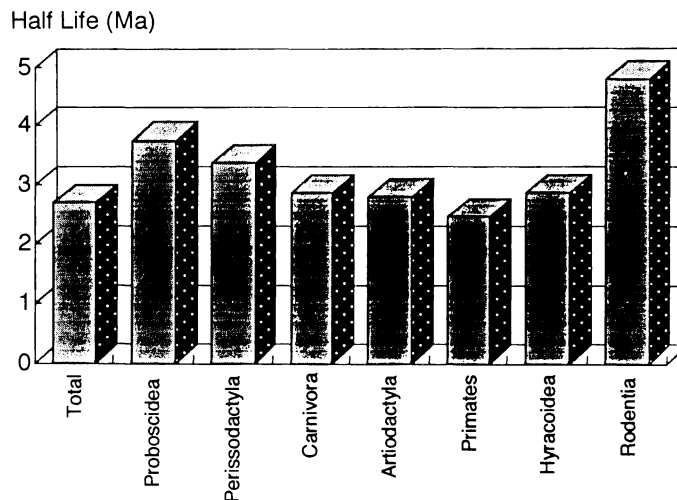
Rodentia has the longest half-life of fauna, but this sample consists of only two taxa. These taxa were added in the Namurungule Fauna. Therefore the half-life of Rodentia is not discussed. Hyracoidea also consists of two taxa, therefore the half-life of this taxon is not discussed in this work. The half-life of Primates (2.46 Ma) is the shortest in the taxa of the Sub-Saharan Africa. Proboscidea (3.75 Ma) has the longest half-life in large mammal (Fig. 16). Kurtén (1972) estimated specific half-life during the Cenozoic Era. In Miocene to early Pleistocene, Proboscidea (2.4 Ma) has the longest half-life and Carnivora (1.6 Ma) has the shortest half-life. The value of half-life of Sub-Saharan Africa is longer than Kurtén’s result. This result is based on the difference of area and taxonomic hierarchy. Because taxonomic hierarchy is used in not only species but also genera in the case of Sub-Saharan Africa. Furthermore, the faunal half-life of taxa from Sub-Saharan Africa seems to be more stable than that from Eurasia.

In the case of half-life of fauna based on each faunal set (stage), half-life of total taxa of Pre-Set I is 3.93 (Faunal Set) stage (7.4 Ma), Set I is 2.82 stage (5.3 Ma), Set II is 2.43 stage (4.6 Ma), Set III is 2.17 stage (4.1 Ma), Set IV is 1.70 stage (3.2 Ma), Set V is 1.62 stage (3.1 Ma), Set VI is 1.66 stage (3.1 Ma), Set VII is 1.56 stage (2.9 Ma) and Set VIII is 1.56 stage (2.9 Ma). The half-life of total taxa on each faunal set decreases to set III and is constant from set IV to VIII in Neogene of Sub-Saharan Africa (Fig. 17). This result indicates large gap of faunal turn over between Faunal Set III and IV and the increasing of the faunal stability after Faunal Set IV (Astaracian) in Sub-Saharan Africa.

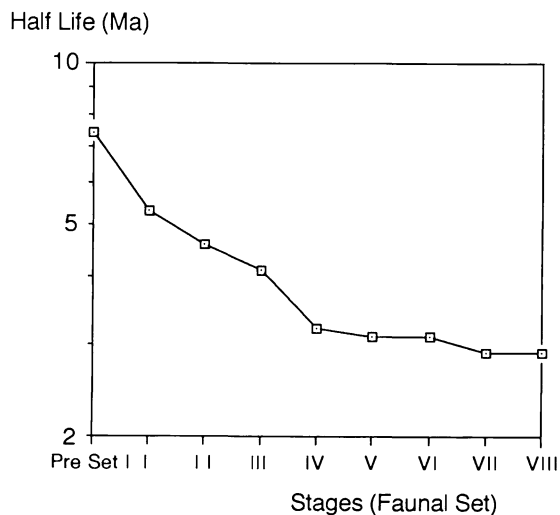
The rise and fall of the total taxa of each Faunal Set from the Neogene Sub-Saharan Africa on the basis of half-life is examined. The following diagram shows the rising and falling curve by a logarithmic scale of each faunal set (Fig. 18). The inclination of rising



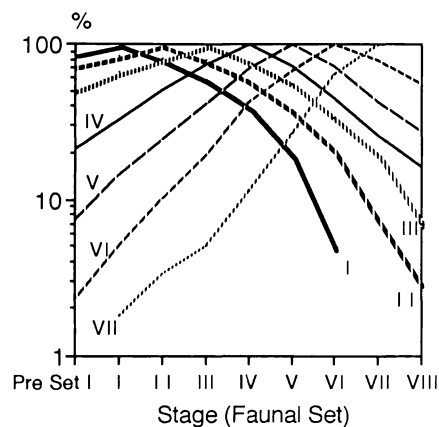
curve is changed to steeper between Faunal Set III and IV. It indicates that the rate of faunal turnover is increased after Faunal Set IV (Astaracian).



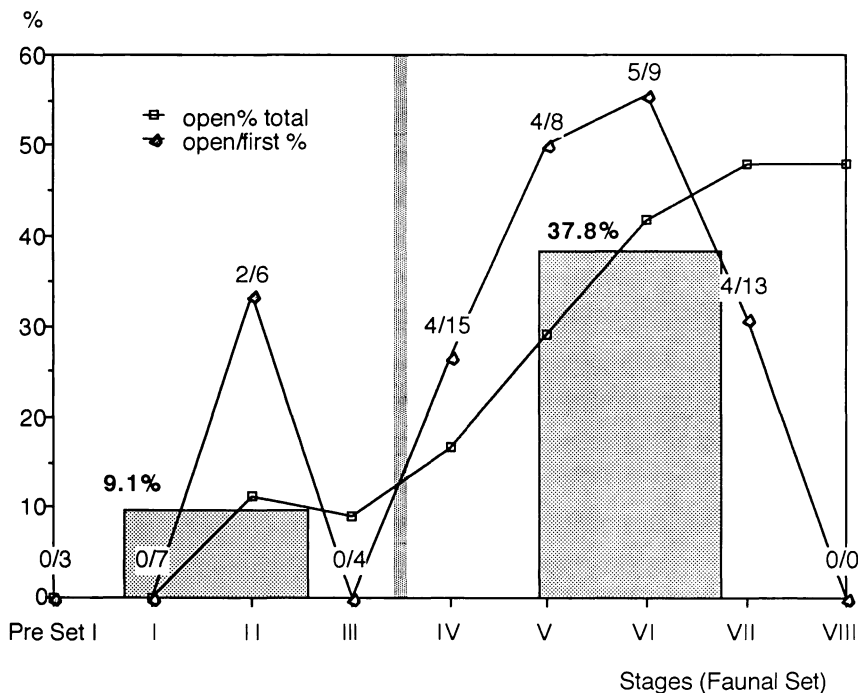
**Fig. 16.** Half-life of the total and each taxa of the mammalian faunas from the Neogene Sub-Saharan Africa.



**Fig. 17.** Half-life of the total taxa of the mammalian faunas from each Faunal Sets of the Neogene Sub-Saharan Africa.



**Fig. 18.** Diagrammatic representation of the rise and fall of the total taxa of Faunal Set I to VII from the Neogene Sub-Saharan Africa on the basis of half-life.



**Fig. 19.** Increase of the open land taxa.

Solid line: percentage of the open land taxa number in the total taxa number. Gray line: percentage of the first appearance open land taxa in the first appearance taxa. Number on the gray line: number of the first appearance open land taxa in the first appearance taxa. Box symbol: average percentage of the open land taxa number by the total taxa number (left: the average percentage during Pre-Set I to Set III, right: the average percentage during Set IV to Set VIII).

As mentioned above, some geological event occurred at late Orleanian to Astaracian (approximately 15-16 Ma). This geological event might be caused by the increasing of the taxa of the indicators (Equidae, Bovidae and some Suidae) of the open-country and/or open woodland environments in the Sub-Saharan Africa. The percentage of the open land taxa number by the total taxa number increases after Faunal Set IV. The number and percentage of the first appearance of open land taxa by the first appearance taxa increases after Faunal Set IV also. The average percentage of the open land taxa number by the total taxa number during Faunal Set IV to VIII (37.8 %) is clearly larger than the average percentage of the open land taxa number by the total taxa number during Faunal Set Pre-Set I to III (9.1 %) (Fig. 19).

## CONCLUSION

### I. Late Miocene Mammalian Interchange of Eurasian and Sub-Saharan Africa

Coryndon & Savage (1973), Thomas (1979, 1981) and Bernor (1983, 1984) emphasized close resemblance between the Miocene Sub-Saharan and Siwalik faunas on the basis of some taxonomic research.

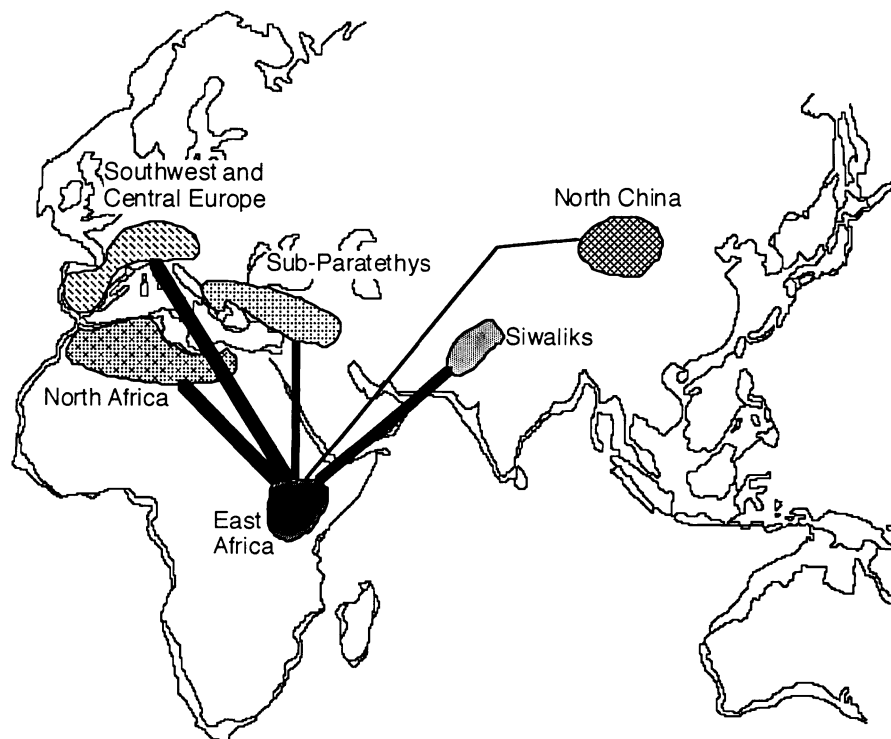


Fig. 20. Faunal resemblance of the Namurungule Fauna and Eurasian faunas.

Phylogenetic research of mammalian taxa of the Namurungule Fauna indicates a similarity to the Turolian faunas from Sub-Paratethys and North Africa. The Miocene mammalian faunas of Sub-Saharan Africa shows resemblance with late Vallesian to Turolian of North Africa, Sub-Paratethys, Southwest and Central Europe faunas based on Simpson's index of faunal resemblance and cluster analysis based on the dissimilarity of mammalian faunas (Fig. 20). The close resemblance between the Miocene Sub-Saharan and Siwalik mammalian faunas should not to be stressed in earlier studies.

## II. Late Miocene Faunal Change of Sub-Saharan Africa

Maglio (1978) briefly states the stability of the Miocene mammalian faunas on the basis of the patterns of faunal evolution of Africa.

Assemblage of the mammalian faunas from early Miocene was comparatively stable and had long half-life in Sub-Saharan Africa on the basis of the results of this work.

However, mammalian assemblage changed drastically at the middle Miocene (Astaracian) in Sub-Saharan Africa. A great number of early to middle Miocene mammalian taxa were extinct and the modern mammalian taxa appeared in this period. The half-life of middle and late Miocene mammalian faunas is shortened compared with the early Miocene faunas in the East Africa. This geological event of faunal turnover occurred by the immigration and divergence of open land taxa. It is evident that the rise of open land taxa is related to the environmental change for the plateau phonolite and basalt volcanism in the middle Miocene East Africa (Pickford, 1981; Williams & Chapman, 1986) and the worldwide warm and arid event (savannitisation) of continental temperate zone in the middle to late Miocene (Liu, 1988). In the middle Miocene (16 Ma) Pacific region, it has been proposed that the tropical event is recognized from shallow marine faunas of the Southwestern Japan (Tsuchi, 1986; Ogasawara, 1988). African and Eurasian land connection was also established before the middle Miocene (16 Ma $\pm$ ) (Bernor et al., 1980). The age of the middle Miocene mammalian turnover indicates similar age of the 21st. peak of periodical extinction of marine animals (Sepkoski, 1986; McGhee, 1989). However, Patterson & Smith (1989) denied periodicity in extinction on the basis of omitting noise component of non-monophyletic group. They considered that some peaks of extinction was recognized on the basis of peaks in diversity. This middle Miocene peak of extinction also suggests the diversity of marine animals followed by marine tropical event.

The Astaracian faunal turnover in Sub-Saharan Africa is considered to be caused by immigration and diversity of open country mammalian taxa and that was related to the worldwide middle Miocene warm event and the plateau volcanism in middle Miocene East Africa.

Furthermore, the Pleistocene and modern taxa and their direct ancestors of Sub-Saharan Africa appeared from the late Miocene faunas of East Africa. It has been made clear that the Namurungule Fauna is the forerunner of the modern Sub-Saharan mammalian fauna of savanna environments.

### III. Application to the Human Evolution

As mentioned before, the Hominoid Fossil was found from the Namurungule Formation. The savannitisation in the Sub-Saharan Africa began in middle Miocene, which is related to the similar condition happened in Eurasian continent from middle to late Miocene. It should be emphasized that the more advanced development and spreading of open-country environments in the Sub-Saharan Africa compared with Eurasian arid event played an important role in the Hominoids evolution. Because, the bipedalism is the most important character of Hominidae which is distinguished from large ape. The origin of bipedalism seems to be closely related to the environmental change from forest to open land (Foley, 1984).

Human evolution in East Africa is accelerated by the savannitisation of Sub-Saharan Africa which commenced earlier than that of Eurasia and continued throughout the Neogene.

### SUMMARY

The Namurungule Fauna indicates a close similarity with the Turolian faunas from Sub-Paratethys and North Africa. The Miocene mammalian faunas of Sub-Saharan Africa shows resemblance with late Vallesian to Turolian of North Africa, Sub-Paratethys, Southwest and Central Europe faunas.

Mammalian assemblage has changed drastically during the middle Miocene (Astaracian). This geological event of faunal turn over is marked by the increase of open land taxa. It indicates the spreading of the warm and arid environments (savannitisation) in the middle to late Miocene East Africa.

Furthermore, the Pleistocene and modern taxa appeared from the late Miocene East African faunas. The Namurungule Fauna is the pioneer of the modern Sub-Saharan mammalian fauna of savanna environments.

The advanced savannitisation in the Sub-Saharan Africa played an important role in the hominization that human ancestors got bipedalism which is caused by their invasion from forest to savanna environments.

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Author's Name and Address: Hideo NAKAYA, Department of Earth Sciences, Faculty of Education, Kagawa University, 1-1, Saiwai-cho, Takamatsu, 760, Japan.

**Appendix 1.** Total taxa of Afro-Eurasian faunas

Taxa	Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<b>Insectivora</b>																							
Soricidae gen. et sp. indet.										1									1				
Crocidae																							
Erinaceidae																							
<i>Galerix atticus</i>															1	1							
<i>Galerix modelingensis</i>															1								
Talpidae																							
<i>Desmanella dubia</i>															1								
<b>Chiroptera</b>																							
Vespertilionidae																							
<i>Samonycteris majori</i>																1							
<b>Lagomorpha</b>										1													
Ochotonidae																							
<i>Alilipus</i> sp.															1								
Leporidae																							
<i>Proloagus</i> cf. <i>crusafonti</i>															1								
<b>Rodentia</b>																							
Rhizomyidae gen. et sp. indet.																			1				
<i>Kanisamys sivalensis</i>																				1	1		
<i>Kanisamys</i> sp.								1															
<i>Rhizomyoides</i> sp.																				1	1		
Sciuridae gen. et sp. indet.																				1			
cf. <i>Atlantoxerus getulus</i>										1													
<i>Spermophilinus</i> cf. <i>bredai</i>																1							
<i>Spermophilinus</i> sp.																							1
<i>Pliopetaurista breessana</i>																							1
<i>Pliopetes</i> sp.																							1
<i>Blackia</i> sp.																							1
<i>Miopetaurista</i> sp.																							1
Ctenodactylidae																							
<i>Sayimys</i> sp.										1													
Castoridae																							
<i>Sinocastor</i> cf. <i>zdanskyi</i>																				1	1		
<i>Dipoides problematicus</i>																							1
<i>Palaeomys castoroides</i>																							1
<i>Palaeomys plassi</i>																							1
<i>Trogonotherium minutum rhenanum</i>																							1
<i>Castor neglectus</i>																							1
Cricetidae																							
<i>Byzantina hellenicus</i>																1							
<i>Byzantina pikermiensis</i>															1								
<i>Copemys</i> sp.																		1					
<i>Kowalskia</i> cf. <i>lavocati</i>															1							1	
<i>Megacricetodon</i> sp.																		1					
aff. <i>Myocricetodon cherifensis</i>										1													
<i>Prosiphneus murinus</i>																					1		
<i>Protatera yardangi</i>										1													
<i>Pseudomeriones pythagorasi</i>																1							
<i>Epimeriones austriacus</i>																							1
<i>Collimys</i> cf. <i>primus</i>																							1
<i>Crocutulodon</i> sp.																							1
Muridae																							
<i>Antemus chinjiensis</i>																			1				
? <i>Gerboa</i> sp.																		1					
cf. " <i>Mastomys</i> " <i>colberti</i>																				1			
<i>Occitanomys</i> ? <i>neutrum</i>															1								
<i>Occitanomys</i> ? <i>provocator</i>															1	1							
<i>Parapodemus gaudryi</i>															1								
<i>Parapodemus lungduensis</i>																							1
<i>Parapodemus</i> sp.																			1				
<i>Pliospalax</i> cf. <i>sotirisi</i>																1							
<i>Progonomys</i> sp.										1													

(cont.)



## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Progonomys</i> sp. nov.																		1				
Hystriidae																						
<i>Hystrix primigenia</i>													1	1								
<i>Hystrix</i> sp.								1									1		1			
Gliridae gen. et sp. indet.																		1				
<i>Muscardinus vireti</i>																					1	
<i>Muscardinus</i> sp.													1									
<i>Myomimus</i> cf. <i>dehmi</i>													1									
<i>Glis</i> cf. <i>minor</i>																					1	
<i>Microdyromys</i> sp.																					1	
<i>Steneofiber jageri</i>												1										
Anomalomyidae																						
<i>Prospalax petteri</i>																					1	
<i>Pterospalax</i> sp.																					1	
Zapodidae																						
<i>Sminthozapus</i> sp.																					1	
Thryonomidae																						
<i>Paraphiomys pigotti</i>																					1	
<i>Paraphiomys</i> sp.																					1	
<i>Paraulacodus</i> sp.																					1	
<b>Primates</b>																						
Lorisidae gen. et sp. indet.																			1			
Hominoidea gen. et sp. indet.								1		1												
cf. <i>Gigantopithecus</i> sp.																			1			
<i>Proconsul</i> sp.																						
<i>Kenyapithecus</i> cf. <i>africanus</i>																						
<i>Ramapithecus punjabicus</i>																			1	1		
<i>Sivapithecus sivalensis</i>																			1	1		
<i>Sivapithecus indicus</i>																			1	1		
Hominoidea gen. et sp. nov.								1														
Hominoidea small form																						
Hominoidea large form																						
Hominidae gen. et sp. indet.																						
<i>Pliohylobates eppelsheimensis</i>													1									
Cercopithecoidea gen. et sp. indet.																				1		
Colobinae gen. et sp. indet.																						
cf. <i>Libypithecus</i> sp.																						
<i>Macaca</i> sp.																						
<i>Mesopithecus pentelici</i>																						
<i>Microcolobus tungenensis</i>																						
<b>Cetacea</b>																						
Delphinidae																						
cf. <i>Lagenorhynchus</i>																						
Platanistidae gen. et sp. indet.																						
<b>Creodonta</b>																						
Hyaenodontidae																						
<i>Dissopsalis carnifex</i>																						
cf. <i>Isohyaenodon</i> sp.																						
<i>Hyainailouros bugtiensis</i>																						
<b>Carnivora</b>																						
Family indet.																						
<i>Agnotherium</i> sp.																						
Amphicyonidae																						
Amphicyoninae large form																						
<i>Amphicyon palaeoindicus</i>																						
<i>Vishnucyon chinjiensis</i>																						
Ursidae																						
<i>Agriotherium</i> cf. <i>africanum</i>																						
<i>Simocyon primigenium</i>																						
<i>Simocyon diaphorus</i>																						
<i>Hyaenarctis</i> sp.																						
<i>Indarctos atticus</i>																						

(cont.)

## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Indarctos lagrelli</i>																					1	
<i>Indactos sinensis</i>																					1	
<i>Ursavus cf. depereti</i>															1							
Mustelidae gen. et sp. indet.							1															
Mustelinae gen. et sp. indet.																		1				
<i>?Enhydriodon laticeps</i>															1							
<i>?Enhydriodon sp.</i>															1							
<i>Eomellivora sp.</i>				1														1				
<i>Eomellivora wimani</i>																					1	
<i>Lutra aonychoides</i>																					1	1
<i>Martes lydekkeri</i>																	1					
<i>Martes palaeosinensis</i>																					1	1
<i>Martes woodwardi</i>														1								
<i>Martes cf. sansaniensis</i>																						1
<i>Martes sp.</i>																	1	1	1			1
<i>Melodon incertum</i>																					1	
<i>Melodon major</i>																					1	
<i>Parataxidea crassa</i>																					1	
<i>Parataxidea maraghana</i>															1	1						
<i>Parataxidea polaki</i>																1						
<i>Parataxidea sinensis</i>																					1	
<i>Plesiogulo brachygnathus</i>																					1	1
<i>?Plesiogulo sp.</i>															1							
<i>Promephitis alexejewi</i>																					1	
<i>Promephitis tartetii</i>															1	1						
<i>Promeles palaeattica</i>															1	1	1					
<i>Promeles sp.</i>																						1
<i>Proputorius minimus</i>																					1	
<i>Sinictis dolichognathus</i>																					1	
<i>Sinictis pentelici</i>															1							
<i>Sivaonyx bathygnathus</i>																						
<i>Sivaonyx sp.</i>							1												1			
<i>Vishnuonyx chinjiensis</i>																		1				
Poccyonidae																						
<i>Sivanasua himalayensis</i>																					1	
Viverridae																						
Viverrinae gen. et sp. indet.																					1	
<i>?Herpestinae sp.</i>																					1	
<i>Herpestes guerini</i>																						
<i>cf. Ichneumia sp.</i>							1															
<i>?Progenetta sp.</i>																					1	
<i>?Viverra chinjiensis</i>																						
<i>Viverra sp.</i>																						
<i>Hyaenidae gen. et sp. indet.</i>		1			1													1	1			
<i>Crocuta sp.</i>								1														
<i>Euryboas sp.</i>																						
<i>Hyaena algeriensis</i>																						
<i>Hyaena honanensis</i>																					1	
<i>Hyaena variabilis</i>																					1	
<i>Hyaenictis (Percrocuta) eximia</i>															1	1	1					1
<i>Hyaenictis graeca</i>																						
<i>Percrocuta tobiensis</i>							1															
<i>Hyaenictitherium sp.</i>															1							
<i>Hypcrrhyaena laekayi</i>								1														
<i>Ictitherium gaudryi</i>																					1	1
<i>Ictitherium hyaenoides</i>																					1	
<i>Ictitherium sinensis</i>																					1	
<i>Ictitherium viverrinum</i>															1	1						
<i>Ictitherium wongi</i>																					1	
<i>Ictitherium robustum</i>																						
<i>Lycyaena dubia</i>															1							
<i>?Miohyena sp. nov.</i>																					1	

(cont.)

## (Appendix 1. cont.)

	Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Palyhaena sivalensis</i>																							1
<i>Percrocuta carnifex</i>																		1	1	1			
<i>Percrocuta gigantea</i>																		1	1				
<i>Percrocuta grandis</i>																		1					
<i>Percrocuta pentelici</i>												1											
<i>Percrocuta senyueki</i>										1													
<i>Plioverrops orbigny</i>														1	1								
<i>Thalassictis hyaenoides</i>														1	1								
<i>Thalassictis wongii</i>													1			1	1						
<i>Thalassictis (Lycyaena) chaeretis</i>														1	1								
<i>Thalassictis (Lycyaena) sp. nov.</i>														1	1								
Felidae gen. et sp. indet.								1									1						
<i>Felis attica</i>														1	1	1							
<i>Felis sp.</i>														1								1	
<i>Homotherium palanderi</i>																				1	1		
<i>Homotherium tingi</i>																				1			
<i>Metailurus parvulus</i>														1	1	1							
<i>Metailurus major</i>														1	1								
<i>Pseudaelurus major</i>																				1	1		
<i>Pseudaelurus minor</i>																				1	1		
<i>Pseudaelurus turnauensis</i>																						1	
? <i>Sansanosmilus</i> sp.																	1						
<i>Sivaelurus chinjiensis</i>																	1						
? <i>Sivamilus</i> (Paramachaerodus) <i>copei</i>																	1						
? <i>Sivaelurus</i> sp.																		1					
<i>Megatereon praecox</i>																		1					
<i>Vinayakia nocturna</i>																		1					
<i>Pontosmilus ogygius</i>														1									
Machairodontinae gen. et sp. inde	1																		1				
<i>Machairodus aphanistus</i>													1										
<i>Machairodus giganteus</i>														1	1	1							
<i>Machairodus cultridens</i>														1									
<i>Machairodus transiensis</i>																						1	
<i>Machairodus</i> sp.											1												
<i>Machairodus</i> sp. A (Paramachaerodus aff. <i>orientalis</i> )											1												
<i>Machairodus</i> sp. B											1												
<i>Machairodus</i> sp. C											1												
<i>Paramachairodus orientalis</i>														1		1							
Felidarm inc. subfam.																						1	
Canidae gen. et sp. indet.								1															
Canidae small form					1																		
Phocidae																							
aff. Monachinae gen. et sp. indet.											1												
<b>Tubulidentata</b>																							
Orycteropodidae																							1
<i>Orycteropus browni</i>																			1				
<i>Orycteropus chemeldoi</i>																							1
<i>Orycteropus gaudryi</i>																1	1						
<i>Orycteropus pligrimi</i>																			1				
<i>Orycteropus</i> sp.								1									1						
<b>Proboscidea</b>																							
Palaeomastodontidae																							
<i>Mammut borsoni</i>															1	1							
Gomphotheriidae gen. et sp. indet.																		1	1	1			
<i>Gomphotherium angustidens</i>															1								
<i>Gomphotherium angustidens</i> var. <i>subtapiroidea</i>															1								
<i>Gomphotherium gigantorostis</i>															1								
<i>Amebelodon cyrenaicus</i>															1								
<i>Anancus cuneatus</i>																						1	
<i>Anancus sinensis</i>																						1	
<i>Anancus</i> sp.																							
<i>Archaeobelodon</i> cf. <i>filoholi</i>								1															

(cont.)

## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Choerolophodon ngorora</i>				1	1		?								1	1	1					
<i>Choerolophodon pentelici</i>															1	1	1					
<i>Selenolophodon spectabilis</i>																					1	
<i>Tetralophodon exoletus</i>																				1	1	
<i>Tetralophodon longirostris</i>																						1
<i>Tetralophodon longirostris</i> var. <i>dubius</i>													1									
<i>Tetralophodon longirostris</i> var. <i>grandis</i>													1									
<i>Tetralophodon</i> sp. nov.	1																					
<i>Tetralophodon</i> sp.				1																	1	
Stagodontidae																						
<i>Stegodon licenti</i>																					1	
<i>Stegodon yushensis</i>																					1	
Elephantidae																						
<i>Primelephas</i> sp.								1														
<i>Stegotetabelodon grandincisivus</i>															1	1						
<i>Stegotetabelodon lybicus</i>											1											
<i>Stegotetabelodon</i> sp.								1	1													
Deinotheriidae gen. et sp. indet.																		1	1	1		
<i>Deinotherium bozasi</i>						1	1	1														
<i>Deinotherium</i> cf. <i>giganteum</i>													1	1	1							1
<i>Deinotherium</i> sp.	1							1											1			
<i>Prodeinotherium hobleyi</i>				1																		
<i>Prodeinotherium</i> sp.		1																				
<b>Hyracoidea</b>																						
Procaviidae																						
<i>Megalohyrax championi</i>		1																				
<i>Parapliohyrax</i> sp.				1	1																	
<i>Pliohyrax graecus</i>															1	1						
<i>Pliohyrax kruppii</i>																1						
<b>Sirenia</b>																						
Dugongidae																						
<i>Metaxytherium serresii</i>										1												
<b>Perissodactyla</b>																						
Equidae (Hipparionine)																						
<i>Hipparion</i> cf. <i>africanum</i>		1				1	1	1		1	1											
<i>Hipparion</i> ( <i>Cremohipparion</i> ) <i>licenti</i>																					1	
<i>Hipparion</i> ( <i>Hipparion</i> ) <i>dermatorhinum</i>																				1	1	
<i>Hipparion dietrichi</i>																1	1					
<i>Hipparion</i> ( <i>Hipparion</i> ) <i>fossatum</i>																				1		
<i>Hipparion</i> ( <i>Hipparion</i> ) <i>hippidiodus</i>																				1		
<i>Hipparion</i> ( <i>Plesiohipparion</i> ) <i>houfenense</i>																					1	
<i>Hipparion matthewi</i>															1	1						
<i>Hipparion minus</i>															1	1	1					
<i>Hipparion</i> ( <i>Probosidhipparion</i> ) <i>pater</i>																				1		
<i>Hipparion proboscideum</i>															1	1						
<i>Hipparion</i> ( <i>Hipparion</i> ) <i>platyodus</i>																					1	
<i>Hipparion</i> cf. <i>sitifense</i>								1		1												
<i>Hipparion turkanense</i>								1	1													
<i>Hipparion</i> ( <i>Cremohipparion</i> ) <i>forstenae</i>																					1	
<i>Hipparion</i> ( <i>Hipparion</i> ) <i>placodus</i>																					1	
<i>Hipparion</i> ( <i>Probosidhipparion</i> ) <i>sinensis</i>																						1
<i>Hipparion</i> ( <i>Baryhipparion</i> ) <i>insperatum</i>																						1
<i>Hipparion</i> ( <i>Baryhipparion</i> ) cf. <i>tchicoicum</i>																						1
<i>Hipparion</i> large form															1	1	1					
<i>Hipparion</i> small form																						
<i>Cremohipparion perimense</i>																			1			
<i>Hipparion prostylum</i>												1										
<i>Hipparion antilopinum</i>																				1		
<i>Hipparion nagriensis</i>																			1			
<i>Hipparion theobaldi</i>																			1	1		
<i>Hipparion primigenium</i>													1									
<i>Hipparion</i> sp.																	1					

(cont.)

## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Anchitherium</i> sp. ( <i>Anchitheriinae</i> )													1									
Chalicotheriidae gen. et sp. indet.	1							1														
<i>Ancylotherium pentelicum</i>															1	1						
<i>Chalicotherium goldfussi</i>													1	1								
<i>Chalicotherium salinum</i>																	1	1				
<i>Macrotherium salinum</i>																	1	1				
Tapiridae																						
<i>Tapirus teilhardi</i>																					1	
Rhinocerotidae gen. et sp. indet.	1																1					
<i>Aprotodon fatehjangense</i>																	1	1				
<i>Brachypotherium lewsi</i>				1				1														
<i>Brachypotherium perimense</i>																	1	1	1			
<i>Brachypotherium goldfussi</i>													1									
<i>Paradiceros</i> sp.	1																					
Aceratheriinae																						
<i>Aceratherium incisivum</i>													1	1								
<i>Aceratherium</i> sp.				1									1				1					
<i>Chilotheridium pattersoni</i>				1																		
<i>Chilotheridium</i> sp.	1							1														
<i>Chilotherium anderssoni</i>																					1	
<i>Chilotherium gracile</i>																					1	
<i>Chilotherium habereri</i>																					1	
<i>Chilotherium intermedium intermedium</i>																	1	1				
<i>Chilotherium intermedium companatum</i>																			1			
<i>Chilotherium kowalewski</i>															1							
<i>Chilotherium persiae</i>																1						
<i>Chilotherium planifrons</i>																					1	
<i>Chilotherium samium</i>															1							
<i>Chilotherium schlosseri</i>															1							
<i>Chilotherium wimani</i>																					1	
Rhinocerotinae																						
<i>Ceratotherium</i> sp.								1														
<i>Dicerorhinus orientalis</i>																					1	1
<i>Dicerorhinus palaeosinensis</i>																					1	1
<i>Dicerorhinus schleiermacheri</i>												1	1	1	1							
<i>Dicerorhinus belvederensis</i>													1									
<i>Dicerorhinus</i> sp.				?								1					1	1				
<i>Diceros neumayri</i>									1													
<i>Diceros pachygnathus</i>															1	1	1					
<i>Rhinoceros broeni</i>																	1					
<i>Rhinoceros cf. sivalensis</i>																				1		
<i>Rhinoceros vidali</i>																			1			
Iranotheriinae (Elasmotheriinae)																						
<i>Caementodon oettingenae</i>																	1	1				
<i>Iranotherium morgani</i>																1						
<i>Kenyatherium bishopi</i>	1							1														
<i>Sinootherium lagrelii</i>																					1	
<b>Artiodactyla</b>																						
Suidae																						
<i>Chleuastochoerus stehlini</i>																					1	1
<i>Conohyus chinjiensis</i>																	1					
<i>Conohyus indicus</i>																					1	
<i>Conohyus sindiense</i>																	1	1				
<i>Conohyus</i> sp.						1															1	
<i>Dicoryphochoerus haydeni</i>																	1	1				
<i>Dicoryphochoerus robustus</i>																					1	
<i>Dicoryphochoerus</i> sp.																					1	
<i>Dorcabune nagrii</i>																	1					
<i>Hippophyus deterrai</i>																					1	
<i>Hippopotamodon sivalense</i> ( <i>Dicoryphochoerus titan</i> )																					1	
<i>Libicochoerus</i> sp. nov.																					1	
<i>Listriodon pentapotamia</i>																	1	1	1			

(cont.)

## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Listriodon</i> sp.													1									
<i>Lophochoerus himalayensis</i>																		1				
<i>Lophochoerus nagrii</i>																		1				
<i>Lophochoerus</i> sp.																	1					
<i>Lopholistriodon kidogosana</i>				1																		
<i>Merycopotamus pusillus</i>																	1					
<i>Microstonyx erymanthius</i>											1		1	1	1	1						
<i>Nyanzachoerus cf. devauxi</i>										1	1											
<i>Nyanzachoerus kanamensis</i>	1									1												
<i>Nyanzachoerus syrticus</i>										1												
<i>Nyanzachoerus tulotos</i>	1							1														
<i>Nyanzachoerus</i> sp.						1	1															
<i>Paleochoerus perimensis</i>																	1	1				
<i>Potamochoerus hytherioides</i>															1							
<i>Potamochoerus hytherioides</i>																			1			
<i>Propotamochoerus hysudricus</i>																			1			
<i>Propotamochoerus salimus</i>																	1	1	1			
<i>Propotamochoerus</i> sp.																			1			
<i>Sus advena</i>																			1			
<i>Sus erymanthius</i>																				1	1	
<i>Sus antiquus</i>													1									
<i>Sus</i> sp.														1								
<i>Tetraodon minor</i>																			1			
<i>Tetraodon</i> sp.																			1			
<i>Tayassuidae</i> gen. et sp. indet.				1																		
<i>Hemimeris</i> sp.	1																					
<i>Schizochocerus</i> sp.																			1			
<i>Anthracotheriidae</i>																						
<i>Hemimeris pusillus</i>																	1	1				
<i>Merycopotamus dissimilis</i>																			1	1		
<i>Merycopotamus petrocchii</i>										1												
<i>Merycopotamus namus</i>																			1			
<i>Hippopotamidae</i>																						
<i>Hexaprotodon sahabiensis</i>										1												
<i>Hippopotamus</i> ( <i>Hexaprotodon</i> ) sp.			1					1	1													
<i>Kenyapotamus coryndoni</i>	1			1	1	1																
<i>Kenyapotamus</i> sp.							1															
<i>Tragulidae</i> gen. et sp. indet.	1																		1			
<i>Dorcatherium chappusi</i>		1																				
<i>Dorcatherium majus</i>																			1	1	1	
<i>Dorcatherium minus</i>																			1	1	1	
<i>Dorcatherium nauti</i>													1		1							
<i>Dorcatherium pigotti</i>		1		1		1																
<i>Dorcatherium</i> sp.																			1	1	1	
<i>Dorcabone anthracotherioides</i>																			1			
<i>Dorcabone nagrii</i>																			1	1	1	
<i>Dorcabone</i> sp.																				1		
<i>Sanitheriidae</i>																						
<i>Diamantohyus africanus</i>		1																				
<i>Climacoceriidae</i>																						
<i>Climacoceras gentryi</i>		1		1																		
<i>Cervidae</i> gen. et sp. indet. large form														1								
<i>Axis speciosus</i>																					1	
<i>Cervavitus demissus</i>																					1	
<i>Cervavitus novorossiae</i>																				1	1	
<i>Eostyloceros blainvillei</i>																					1	
<i>Eostyloceros triangularis</i>																					1	
<i>Muntiacus</i> sp.																1						
<i>Pliocervus pentelici</i>														1	1	1						
<i>Procapreolus latifrons</i>																				1	1	
<i>Giraffidae</i>																						
<i>Giraffa</i> sp.								1														

(cont.)

## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Giraffokeryx punjabiensis</i>																	1	1				
<i>Giraffokeryx</i> sp.																	1					
<i>Helladotherium duvernoyi</i>														1	1	1						
<i>Helladotherium</i> sp. nov.															1							
<i>Honanotherium atticum</i>														1		1						
<i>Honanotherium schlosseri</i>																					1	
<i>Honanotherium speciosum</i>														1	1							
<i>Hydaspiatherium megacephalum</i>																		1	1			
<i>Palaeotragus coelophrys</i>															1	1				1		
<i>Palaeotragus decipiens</i>																					1	
<i>Palaeotragus microdon</i>																				1		
<i>Palaeotragus rouenii</i>														1	1							
<i>Palaeotragus primaevus</i>					1	1	1	?														
<i>Palaeotragus</i> sp. nov.	1																					
<i>Palaeotragus</i> sp.																					1	
<i>Samotherium boissieri</i>														1	1							
<i>Samotherium sinense</i>																				1		
<i>Samotherium</i> sp.	1			1						1												
cf. <i>Sivatherium</i> sp.																		1				
? <i>Walangania africanus</i>			1																			
Bovidae																						
<i>Dorcadoryx triguetricornis</i>																					1	
<i>Homoiodorcas tungenium</i>				1																		
<i>Kubanotragus sokolovi</i>																	1					
<i>Leptobos syrticus</i>										1												
<i>Helicoportax tragelaphoides</i>																	1	1				
<i>Helicoportax praecox</i>																	1	1				
<i>Pachyportax latidens</i>																		1	1			
<i>Pachyportax</i> sp.																		1				
<i>Paraprotoryx minor</i>																				1		
<i>Paraprotoryx killgusi</i>																					1	
<i>Plesiadax depereti</i>																				1		
<i>Plesiadax minor</i>																				1		
<i>Protragocerus gluten</i>																	1					
<i>Protragocerus labidotus</i>				1																		
<i>Sinoryx bombifrons</i>																					1	
<i>Strepsipotax</i> sp.																	1					
<i>Sivaceros</i> cf. <i>gradiens</i>																	1	1	1			
<i>Sivoreas eremita</i>					?		?										1					
<i>Tragocerus browni</i>																		1	1			
<i>Tragocerus gregarius</i>																					1	
<i>Tragocerus lagrelii</i>																					1	
<i>Tragocerus laticornis</i>																						1
<i>Tragocerus punjabicus</i>																		1	1			
<i>Tragocerus spectabilis</i>																					1	
Alcelaphini gen. et sp. indet.								1	1													
cf. <i>Aepycerus</i> sp.								1														
cf. <i>Damalacra</i> sp.										1												
Antilopini gen. et sp. indet.								1	1		1											
<i>Antidorcas</i> sp.				1		1																
<i>Gazella altidens</i>																					1	
<i>Gazella capricornis</i>													1	1								
<i>Gazella deperdita</i>																1						
<i>Gazella dorcadoidea</i>														1							1	
<i>Gazella gaudryi</i>																					1	1
<i>Gazella lydekkeri</i>																	1	1	1			
<i>Gazella mytilinii</i>															1							
<i>Gazella paotehensis</i>																					1	
<i>Gazella</i> sp.	1							1	1								1	1				
<i>Oioceros atropatenes</i>																	1					
<i>Oioceros rodleri</i>																		1				
<i>Oioceros rothi</i>														1			1					

(cont.)

## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Oioceros wegneri</i>															1							
<i>Oioceros</i> sp.				1		1															1	
<i>Oiuzoceros</i> sp.	1																					
<i>Prosinotragus kuhkmanni</i>															1							
<i>Prosinotragus</i> sp. nov.															1							
<i>Prostrepsiceros houtumschindleri</i> var. A															1							
<i>Prostrepsiceros houtumschindleri</i> var. B																1						
<i>Prostrepsiceros</i> (P.) libycus										1												
<i>Prostrepsiceros rotundicornis</i> var. A														1								
<i>Prostrepsiceros rotundicornis</i> var. B															1	1						
<i>Protragelaphus skouzesi</i>														1	1							
<i>Sinotragus crassicornis</i>															1							
<i>Sinotragus wimani</i>																				1		
<i>Sinotragus</i> sp. nov.																1						
Boselaphini gen. et sp. nov.																		1				
Cephalophini gen. et sp. indet.								1														
Hippotragini gen. et sp. indet.						1	1	1	1													
<i>Hippotragus</i> sp.										1												
Miotragocerus-Tragoportax Complex																						
<i>Miotragocerus cyrenaicus</i>										1												
<i>Miotragocerus gradiens</i>																	1					
<i>Miotragocerus monacensis</i> var. A															1	1						
<i>Miotragocerus monacensis</i> var. B															1	1	1					
<i>Miotragocerus punjabicus</i>																		1				
<i>Miotragocerus valenciennesi</i>															1	1						
<i>Miotragocerus</i> sp.	1																					
<i>Samokeros minotaurus</i> var. A																1	1					
<i>Samokeros minotaurus</i> var. B																	1					
<i>Tragoportax amalthea</i>															1	1						
<i>Tragoportax curvicornis</i>																1						
<i>Tragoportax rugosifrons</i>															1	1						
<i>Tragoportax salmontanus</i>																			1			
<i>Tragoportax</i> sp.																			1			
Neotragini gen. et sp. indet.								1														
<i>Raphicerus</i> sp.										1												
Ovibovini gen. et sp. indet.																						
<i>Criotherium argalioides</i>																1						
<i>Palaeoreas lindermayeri</i>															1	1						
<i>Palaeoreas</i> sp.					?		?															
<i>Parumiatherium rugosifrons</i>																1						
<i>Urmaitherium intermedium</i>																				1		
<i>Urmiatherium polaki</i>																	1					
Palaeoryx-Protoryx Complex																						
<i>Palaeoryx pallasii</i> var. A															1							
<i>Palaeoryx pallasii</i> var. B																1						
<i>Palaeoryx pallasii</i> var. C																1	1					
<i>Palaeoryx pallasii</i> var. D																1	1					
<i>Protoryx carolinae</i>																1						
<i>Protoryx crassicornis</i> var. A																1	1					
<i>Protoryx crassicornis</i> var. B																	1	1				
<i>Protoryx laticeps</i> var. A																	1	1				
<i>Protoryx laticeps</i> var. B																	1	1				
<i>Protoryx laticeps</i>	1																					
<i>Protoryx</i> sp.						1																
<i>Protoryx shansiensis</i>																				1		
<i>Protoryx bohlini</i>																					1	
<i>Protoryx yuchensis</i>																						1
<i>Pseudotragus capricornis</i>																1						
<i>Pseudotragus</i> ? gentryi						1	1															
? <i>Pseudotragus potwaricus</i>																		1				
? <i>Pseudotragus</i> sp.																			1			
<i>Sporadotragus parvidens</i>																1	1					

(cont.)



## (Appendix 1. cont.)

Site	NM	AA	KG	NG	NE	NW	NK	LK	MP	SB	BH	ML	EP	PK	SM	MG	CJ	NR	DP	BD	YS	DD
<i>Tragoreas oryxoides</i>															1							
<i>Tragoreas palaeosinensis</i>																					1	
<i>Pachytragus aff. solignaci</i>				1																		
<i>Reduncini</i> gen. et sp. indet.						?	?	1														
<i>Redunca aff. darti</i>										1												
<i>Rupicapriini</i> gen. et sp. indet.															1							
<i>Tragelaphini</i> gen. et sp. indet.								1	1													
<i>Selenoportax lydekkeri</i>																		1	1			
<i>Selenoportax vexillarius</i>																			1			
<i>Selenoportax sp.</i>														1					1			
<b>Total Number of Taxa</b>	23	14	1	33	7	10	11	29	9	44	5	9	22	73	85	42	66	95	28	60	51	30

NM; Namurungule, AA; Aka Aiteputh, KG; Kongia, NG; Ngorora, NE; Ngorora upper E, NW; Ngeringerowa  
 NK; Nakali, LK; Lukeino, MP; Mpesida, SB; Sahabi, BH; Bou Hanifia, ML; Mt. Lebéron, EP; Eppelsheim  
 PK; Pikermi, SM; Samos, MG; Maragheh, CJ; Chinji, NR; Nagri, DP; Dhok Pathan, BD; Baode, YS; Yushe  
 DD; Dorn-Dürkheim.